

**Investigation of the biodiversity and ecology of encrusting
epifauna associated with bivalve molluscs in the North-East
Atlantic and Qatar**

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Abstract

Biogenic reefs provide hard substrates in areas that would otherwise be dominated by sediment. These reefs support a diverse assemblage of suspension feeders such as barnacles, tube worms, and bryozoans. The aim of this study is to investigate the factors influencing biodiversity, abundance, competition, spatial distribution and successional patterns of encrusting epifaunal communities in temperate and tropical regions. These include the *Modiolus modiolus* reefs of the North- East Atlantic temperate zone and the coral reefs and pearl oyster reefs in Qatar. In both areas, the encrusting epifaunal community was recorded, species identity confirmed with selected SEM imagery. The species abundance and competition data was analysed by multivariate approaches to give an understanding of the community complexity of horse mussel shell epifauna, and related to the micro-environmental and biogeographic context. The present study provides the first formally described taxonomical information on bryozoan fauna collected from Qatar that are exposed to extremes in temperature and salinity. Twenty-five species of bryozoans are reported from across the coastline of Qatar. These species belong to twenty-four genera in twenty-two families of the orders Ctenostomata and Cheilostomata. High precision Nonius X-ray Diffractometer was used to determine the mineral composition of Qatar Bryozoa to baseline our knowledge of Qatar bryozoan calcification and start to consider how they endure extreme ocean climate, specifically the combination of high temperature and salinity.

Dedication

To the candles which have melted with pride

To enlighten each step in our life

To ease every burden in front of us

The messengers of knowledge and behavior

Thank you, my esteemed parents

Thank you for your constant support

You have drawn me the future, with the lines of hope and confidence

God bless you.

Acknowledgments

To that precious land in which I was born and brought up.

My nation (Qatar), the sincere thanks and appreciations are extended to you and also my thanks are conveyed to His Highness ShkTamim Bin Hamad Al Thani who has been supporting the knowledge and scholars and calling for the renaissance and independence. To you, my nation, I dedicate my knowledge and service; you are the first choice for me.

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3. *Aeta ligulata*
4. *Biflustra* sp.
5. *Parellisina* sp.
6. *Akatopora* sp.
7. *Smittipora harmeriana*
8. *Odontoporella* sp.
9. *Predanophora longiuscula*
10. *Caulibugula* sp.
11. *Puellina egretta*
12. *Poricella robusta*
13. *Drepanophora indica*
14. *Trypostega johnsoulei*
15. *Chorizopora brongniartii*
16. *Thalamoporella granulata*
17. *Exechonella brasiliensis*
18. *Parasmittina raigii*
19. *Parasmittina egyptiaca*
20. *Parasmittina spondylicola*
21. *Schizoporella errata*
22. *Microporella orientalis*
23. *Rhynchozoon* sp.
24. *Celleporaria* sp.1
25. *Celleporaria* sp.2

Glossary for the Bryozoa

Adventitious avicularium: an avicularium originated from one or more marginal frontal pores and positioned on the surface of a zooid.

Ancestrula zooid: the first zooid of the colony, formed by metamorphosis of a larva. In some species, the ancestrular zooids may be twinned, triple, or a group of six.

Anter: part of the orifice distal to the condyles in ascophoran Cheilostomata.

Areola: a marginal opening in the frontal calcification leading to an areolar pore in ascophoran cheilostomatates.

Ascopore: a frontal pore which serves as the inlet to the ascus in some ascophoran Cheilostomata.

Autozooid: the feeding zooid in Bryozoa.

Avicularium: specialized zooid in the Cheilostomata with reduced polypide but has strong muscles which operate a modified operculum called mandible.

Brood chamber: chamber for the brooding of larvae; includes in cyclostome it is called gynozoids and in cheilostome ovicells.

Colony form: general shape and habit of a bryozoan colony.

Communication pore: the opening in interzooidal wall.

Condyle: one of a pair of oppositely placed protuberances situated beneath the operculum in cheilostomes.

Costa: one of the spines forming an arch over the frontal membrane in cribrimorph cheilostomes; usually joined together with the neighboring costae to form a frontal costate shield.

Cryptocyst: horizontal calcareous lamina on the basal side of the frontal membrane, developed from the vertical walls of the zooid of anascan cheilostomes.

Ectooecium: the outer calcified layer of ooecial wall.

Entooecium: the inner membranous layer of ooecial wall.

Foramen: an un-calcified opening in the frontal wall with direct communication from the external environment to the space between the calcified frontal wall and the frontal membrane.

Frontal membrane: un-calcified part of frontal body wall in Cheilostomata.

Frontal shield: the calcified frontal surface of ascophoran zooids.

Frontal wall: a calcareous frontal body wall in cheilostomes.

Gymnocyst: in anascan cheilostomes, the part of the calcified frontal wall between the frontal membrane and the free edges of the vertical wall.

Heterozooid: specialized non feeding zooid.

Internode: in erect colonies, internodes are the sections bearing autozooids, joined by un-calcified or poorly calcified connecting tubes.

Kenozooid: heterozooid without orifice or muscles.

Lateral wall: In cheilostomes, vertical skeletal walls between adjacent rows of zooids.

Lyrula: opercular tooth, often anvil-shaped, on the proximal side of the orifice in some Cheilostomata.

Mandible: apart of an avicularium, moved by muscles.

Operculum: un-calcified lamina or flap, hinged on condyles, which closes the zooidal orifice in Cheilostomata.

Opesia: the opening below the frontal membrane in zooids of anascan Cheilostomata.

Opesiule: small openings or pores in the cryptocyst proximal to the opesia in anascan cheilostomes.

Orifice: the opening in the zooid wall through which the lophophore and tentacles are protruded.

Ovicell: the globular brood chamber in Cheilostomata.

Peristome: in cyclostomes: a tubular prolongation around the zooidal aperture. In cheilostomes:
a rim surrounding the primary orifice.

Poster: part of the orifice in ascophoran Cheilostomata proximal to the condyles.

Rhizoid: zooid weakly calcified, modified as a rootlet, for stabilizing a colony to the substrate, or for reinforcing a branch, or for connecting across branches of a colony.

Rostrum: spike-like prolongation of an avicularium.

Setiform: avicularian mandibles which are thin and long,

Sinus: slit at the proximal edge of orifice in some ascophoran cheilostomes.

Spiramen: an opening in the external frontal calcification proximal to the orifice.

Stolon: a rod-like structure parallel to the zooidal growth directions in stenolaemates.

Umbo: a prominence on the frontal wall proximal to the orifice in cheilostomes.

Zooecium: the skeleton of bryozoan zooid.

Zooid: a single bryozoan individual of a colony.

1. Chapter 1: General introduction

In the marine environment, biogenic reefs have an important role as ecosystem engineers through their influence on nutrient cycling, water filtration, habitat structure, and biodiversity. These reefs are inhabited by a diverse and abundant community of invertebrates and fishes that use the structural complexity of the reefs as a refuge from predation and environmental stresses (McLeod et al., 2013). Many bivalve reefs have declined precipitously, some to commercial extinction (Thurstan et al., 2013). For example, in a review of oyster reefs worldwide, Beck et al. (2011) estimated that 85% of oyster reefs have been lost globally and most of the remaining reefs were in poor condition. Reef declines are due to overfishing and an overall decline in the condition of coastal waters through impacts such as sedimentation, and habitat disturbance (McLeod et al., 2013). Environmental monitoring often targets benthic invertebrates as their presence reflects the habitat conditions over long periods (Campbell, 2017). Studying the ecology of community development and species abundance of benthic invertebrates is important to understand the mechanisms linking changes in the marine environment and the distribution and abundance of marine organisms to their habitat.

1.1. Definition of biogenic reefs

Biogenic reefs have important effects on the physical marine environment, they stabilise sands, gravels and stones; the shells or tubes of the organisms themselves provide hard substrata for attachment of sessile organisms; they also provide a diversity of surfaces and sediments for colonisation; and accumulated faeces, pseudo-faeces and other sediments may be an important source of food for other organisms, therefore many biogenic reefs have a very rich associated fauna that is important both as a fishery, and as a source of food for birds and for many benthic predators (Holt et al., 1998).

Biogenic reefs have been defined as *“Solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms”* (Holt et al., 1998).

Modiolus modiolus (Linnaeus, 1758) horse mussel reefs are considered a type of Annex I biogenic reef under the Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora) (Gormley et al., 2015). *Modiolus modiolus* reefs occur in two main physical forms: semi-infaunal reefs, which grade in density and thickness from continuous dense, raised reefs to scattered clumps which may not actually fit the definition of biogenic reefs; and a more unusual infaunal gravel-embedded reef community which can form wave like mounds up to 1 metre high. *Modiolus modiolus* has a predominantly northern and western distribution in the United Kingdom, with few reef areas known south of the Humber or Severn. A number of cSACs include semi-infaunal *Modiolus* reefs, but the infaunal gravel-embedded reef community has only been identified outside UK waters. *Modiolus modiolus* occurs in a wide variety of biotopes. Infaunal reefs have been reported in strong tidal waters of moderate depths (15-40 m). Semi-infaunal reefs and beds occur in a variety of situations on mixed or muddy sediments and in a variety of current regimes, mainly between the shallow infralittoral and around 50 m. *Modiolus* reef communities are often patchy but may be extensive, covering many hectares. *Modiolus modiolus* is a very long-lived species and animals in reef communities are frequently 25 years old or more. Spawning seasons are variable with depth and location and fertilized individuals live the first stage of their life as planktonic larvae for 3 or 4 weeks then they settle, attach to a substrate, and metamorphose into juveniles (De Schweinitz and Lutz, 1976).

Although reefs in enclosed sea lochs are probably self-recruiting, those from more open areas may not be. Predation rates, especially by crabs and starfish, are high in the early years. *Modiolus* does not mature sexually until it is 3 to 6 years old, allowing all of its efforts to be directed into rapid growth in the early years after which it is less vulnerable to predation. *Modiolus* has a very strong structuring influence on the sediments in which reef areas usually occur, and extremely rich associated faunas containing hundreds of species have been found (Holt et al., 1998).

1.2. *Modiolus modiolus*

Modiolus modiolus is a large mussel growing to 22 cm long with thick, irregularly oval or rhomboidal shell outline (Figure 1.1). The shell is bluish white in colour, darkening in larger specimens; the periostracum is very glossy. The inner surface of the shell is white, sometimes with a faint bluish tinge towards posterior margin. The internal animal colour is dark orange; the foot is red, turn to white towards the thick and wrinkled base. Both margins of the mantle

are without toothed fringe and covered with delicate cilia (Hayward et al., 1990). *M. modiolus* are found part buried in soft sediments or coarse grounds or attached to hard substrate by byssus threads, forming clumps or extensive beds or reefs (Walters, 2007). *M. modiolus* habitat is distributed from the lower shore to about 150 m depth.



Figure 1.1: Example of a horse mussel *Modiolus modiolus* from Ramsey Bay, Isle of Man (scale bar = 10 cm).

Modiolus modiolus shell is characteristically inequilateral; the posterior shell margin is enlarged and rounded whereas the anterior shell margin is less rounded and projects only slightly anteriorly beyond the umbones. The antero- and posterodorsal shell margins are steep (the former slightly curved) and meet at a mid-dorsal apex. In the dorsal view (Figure 1.2B), the external, opisthodetic ligament (l) extends posteriorly from the umbones (u) for not quite half the length of the shell. In the ventral view the margin is almost straight and there is no significant byssal gape (Figure 1.2C). From the anterior aspect (Figure 1.2D), the shell is pointed dorsally but laterally swollen ventrally, with the ligament (l) arising from the umbones (u) located approximately half way along the dorsoventral axis of the shell. The shell is also widest (Figure 1.2D, x–y) at this level. From the posterior aspect (Figure 1.2E), the margins of the valves are united everywhere with no marginal crenulations (Dinesen and Morton, 2014).

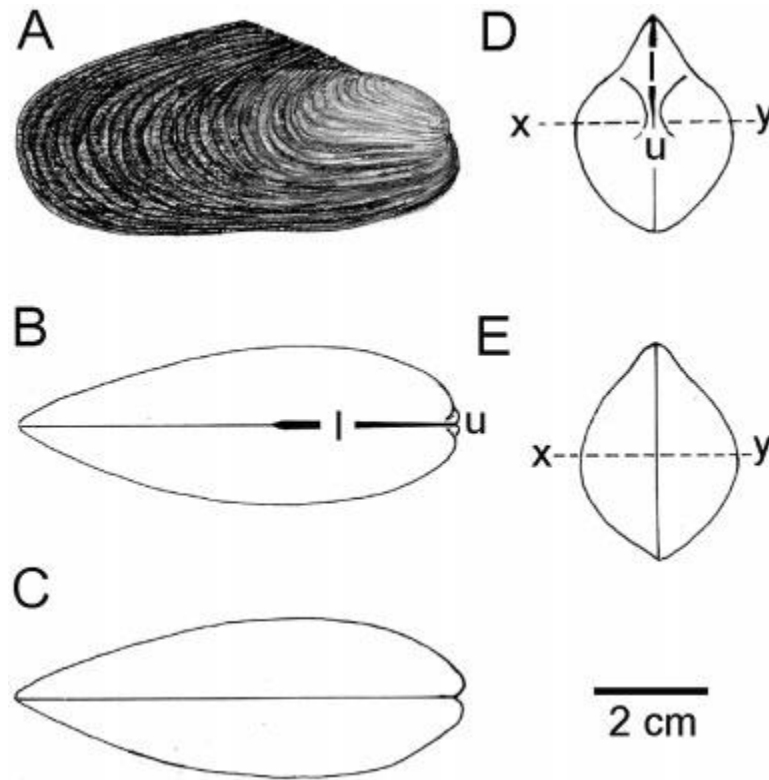


Figure 1.2: Horse mussel *Modiolus modiolus* shell view from various aspects. A: an external view of the right shell valve; B: a dorsal view; C: a ventral view; D: an anterior view; and E: a posterior view (x–y represents the point of greatest shell width) (Dinesen and Morton, 2014).

1.3. *Modiolus modiolus* beds

Hard substrates, including skeletons of living and dead organisms as well as rock clasts, may be colonised by a diverse array of organisms (Santos et al., 2008). Many benthic systems, including sea-grass meadows, coral reefs, oyster reefs and mussel beds are characterised by the presence of species that form biogenic habitats (Ragnarsson et al., 2012). Organisms living amongst these habitats are from a wide range of taxa, including sessile species such as sponges, bryozoans and ascidians, and mobile species such as polychaete worms and crabs (Bunting, 2010).

Horse mussels are common on UK coasts, and are important to conservation where they form extensive beds in sandy and muddy seascapes (JNCC, 2015). The horse mussel *M. modiolus* forms dense beds, at depths up to 70 m, mostly in fully saline conditions and often in tide-swept areas. Although *M. modiolus* is a widespread and common species, horse mussel beds are more limited in their distribution. *M. modiolus* beds are found on a range of substrata, from cobbles through to muddy gravels and sands, where they tend to have a stabilising effect, due to the production of byssal threads. Communities associated with *M. modiolus*

beds are diverse, with a wide range of epibiota and infauna, including hydroids, red seaweeds, bivalves, soft corals, anemones, barnacles, and bryozoans (OSPAR Convention, 2015). Horse mussel beds are found in Shetland, Orkney, the Hebrides and other parts of western Scotland, the Ards Peninsula, and Strangford Lough, the Isle of Man, north-west Anglesey and North Llŷn. *M. modiolus* beds have been reported from both the North Atlantic and North-East Pacific coastal shelf areas (Dinesen and Morton, 2014).

Horse mussel beds are good indicators of ecosystem conditions. They furnish important ecosystem services by forming complex habitats, stabilizing sediments, filtering water, recycling nutrients, sequestering of carbon and indicate water quality and habitat conditions over long time periods (Kreeger et al., 2010). Kent et al. (2017) reported that *M. modiolus* promote the abundance of associated epifauna, as well as being capable of doubling the flow of suspended particulate matter from the water column to the benthos in a process that controls coastal turbidity levels. Further studies by Kent et al. (2016) have shown these beds to also support greater populations and nursery habitats for commercially important species. Horse mussels are typically long-lived up to 35 years (but can be 68 years) and slow growing, and so are vulnerable to disturbance (Anwar et al., 1990). Horse mussels themselves are not widely collected for food, but the beds have been extensively damaged by scallop dredging and trawling. Horse mussel beds are also threatened by aggregate extraction, dredge spoil dumping, cable laying and other activities that cause serious seabed disturbance. Pollution and the increasing water temperature resulting from climate change may also be a threat (JNCC, 2015).

1.4. *Modiolus modiolus* conservation priority

The horse mussel *M. modiolus* in some places forms very dense beds that can carpet the sea floor or build up as reef like features or bioherms (Holt et al., 1998). These localised features are of considerable conservation interest, coming within the reef category of the EU Habitats Directive and they are listed as a Priority Feature by OSPAR. The nomination of *M. modiolus* beds to be placed on the OSPAR List was on the basis of an evaluation of their status according to the Texel-Faial Criteria, which noted the sensitivity, and physical disturbance, of these biogenic habitats (OSPAR, 2003). Moreover, horse mussels often form localised areas of high biodiversity and productivity on parts of the seabed. *M. modiolus* beds are known to be highly vulnerable to physical disturbance and once destroyed beds do not seem to recover naturally in the medium term (Rees, 2005). Suding and Hobbs (2009) define resilience to

disturbance as “the amount of disturbance a system can endure while retaining the same ecological structure, function and feedbacks”. High rates of disturbance reduce the abundance of biogenic reefs and the diversity of associated epifaunal communities, which have disproportionately high contributions to ecosystem function (Lundquist et al., 2010). A study by Lundquist et al. (2010) investigated the effect of disturbance on colonization processes in marine benthic systems and reported that disturbance causes the clearing of a patch in the marine system that is often unsuitable for immediate colonization by mussels due to their life history, in terms of larval dispersal and reaching maturity to the minimum age to serve as a colonisation source for epifaunal species.

Current and potential threats to *M. modiolus* such as fishing, particularly using trawls and dredges for scallops, is known to have caused widespread and long-lasting damage to beds in Strangford Lough and off the south-east of the Isle of Man (Holt et al., 1998). Cook et al. (2013) investigated the effects of single passes of bottom-towed fishing gear on rare protected *Modiolus modiolus* reef communities and reported that there was a significant decline in epifaunal species abundance in response to both trawl and scallop dredges as well as declines in all major taxonomic groups in the epifaunal community at the trawled site. The study also reported that the recovery of *Modiolus modiolus* reef was observed after a year of the recorded disturbance as well as a change in the epifaunal community.

1.5. *Modiolus modiolus* clumping behaviour

In the natural environment, mussels clump together to form large, dense dynamic structured reefs composed of constantly re-arranging individuals. Mussels living at the centre of a bed are more sheltered from predation and physical disturbance than individuals living at the bed edge or solitary mussels (Nicastro et al., 2007).

Holt, et al., (1998) described two types of *Modiolus modiolus* reef forms, semi-infaunal reefs when large accumulations of faecal mud and shell build up and living mussels form an irregularly clumped layer over the mound, where the largest living individuals are buried about two thirds of their length in the deposit and small individuals find refuge amongst the byssal threads of the clumps of larger ones. The other type is infaunal reefs that occur on coarser grounds and in strong currents, where the mussels bind gravel together and live as nested infauna within the coarse deposit to form wave-like mounds or bioherms. The best described examples of the latter within Britain are those off the north east of the Isle of Man,

where the *M. modiolus* are concentrated and the associated fauna much richer (Holt et al., 1998).

Modiolus modiolus shell is pointed dorsally and widest in the middle of dorsal-ventral region at a point approximating the position of the umbones, this could reflect the wave-exposed habitat-forming lifestyles adopted by this species that crowd together basally but have to maintain a long extent of projecting shell to facilitate feeding and respiration (Dinesen and Morton, 2014).

1.6. *Modiolus modiolus* filter feeding

M. modiolus beds are important habitats with many ecosystem functions that can support numerous species. The filter feeding of the mussels provide essential food sources to higher and commercially important organisms, control of phytoplankton dynamics, as well as the suspended material and hence water clarity, light penetration and the distribution of particles within the water column (Hutchison et al., 2016; Strong et al., 2016). In *Modiolus modiolus* the exhalant siphon comprises a low, unadorned, cone. They are situated posterior to the posterior adductor muscle and approximates in its dorsal-ventral dimensions. The inhalant apertures are long, not separated from the pedal gape by pallial fusions, and are marginally apapillate (Figure 1.3) (Dinesen and Morton, 2014).

In densely aggregated *M. modiolus* biogenic reefs, mussels concentrate large amounts of suspended particle matter and transfer this material to the benthos through secondary production and the rejection of biodeposits faeces and pseudofaeces (Kent et al., 2017). These deposits accumulate within these biogenic structures and provide a favorable environment for a rich and abundant assemblage of infaunal and epifaunal deposit feeders. These biogenic structures are also colonized by surface suspension feeders such as bryozoans and polychaete tube worms that benefit from the lowered, turbulent, current conditions generated by *M. modiolus* filter feeding (Strong et al., 2016).

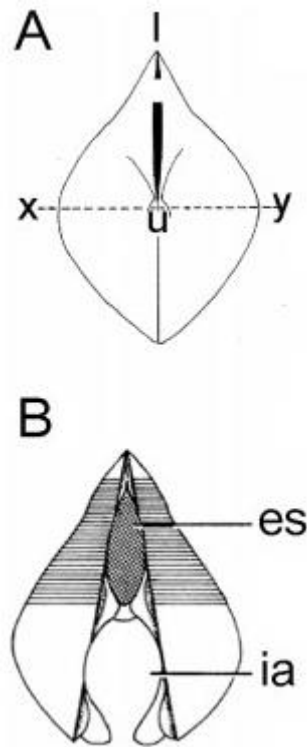


Figure 1.3: Horse mussel *Modiolus modiolus* shell posterior region. A: posterior view (x–y represents the point of greatest shell width), B: the siphons (es: exhalant siphon, ia: inhalant apertures) (Dinesen and Morton, 2014).

1.7. Shell size

Mussel beds harbor a variety of benthic communities in spaces provided by mussel shells. This biogenic system is a good example for investigating the coexistence of many species in an ecological island. Community structure and the dynamics of benthic animals associated with mussel beds are controlled by factors including age or size structure of mussels, and the amount of fine particles around the bed (Tsuchiya, 2002).

Modiolus modiolus is the largest British marine mussel and is capable of growing to 15-22 cm in shell length (Anwar et al., 1990). Anwar et al. (1990) reported that *Modiolus modiolus* growth rate is very rapid in the first four to six years, and when the shell reaches a length of 35-40 mm they are less vulnerable to attack by predators. Only the very largest crabs and starfish can open mussels over 50 mm in length, and large *Modiolus* are thought to be relatively predator free since the main predator, the fish Cod (*Gadus gadus*) numbers have been seriously reduced by overfishing.

1.8. Encrusting epifauna on *Modiolus modiolus* horse mussels

1.8.1. Bryozoa

Species in the phylum Bryozoa comprise small to microscopic but fascinating and often beautiful animals that build intricate colonies. Despite the fact that there are about 8000 living species, the Bryozoa remain largely unknown to most people. Bryozoans have been placed into three classes: (1) Phylactolaemata, (2) Stenolaemata that includes the order Cyclostomata and (3) Gymnolaemata, that includes orders Ctenostomata and Cheilostomata. Bryozoans or moss animals are all marine animals, except for the freshwater bryozoans of the class Phylactolaemata (Boardman et al., 1987; McKinney and Jackson, 1989).

Bryozoans can reproduce both sexually and asexually. Asexual reproduction occurs by budding off new zooids as the colony grows and expands in size. If a piece of a bryozoan colony breaks off, the piece can continue to grow and will form a new colony (Buchsbaum et al., 1987). A bryozoan colony begins with a single individual, known as an ancestrula. Ancestrulas are sexually produced, but colonies grow through asexual reproduction. Breeding is regulated by water temperatures and levels of sunlight; increasing temperatures and light activate phytoplankton growth that generates colony budding and, sexual reproduction. Species may free-spawn or, females will brood eggs for a short time. Larvae of brooding species settle quickly following hatching, as their larval forms cannot feed. However, other bryozoan species do not show brooding behaviour, and release gametes into the water (Brusca and Brusca, 2003).

Bryozoans are found on all types of hard substrates such as sand grains, rocks, shells, wood, and on softer surfaces such as blades of kelps and other algae (Buchsbaum et al., 1987). Others like the fossil bryozoans form lacy or fan-like colonies and may form an abundant component of limestone. It should be noted that, bryozoan colonies range from millimetres to meters in size, but the individuals or zooids that make up the colonies are rarely larger than a millimetre and these colonies may be mistaken for hydroids, corals, or even seaweed.

Marine bryozoans secrete hard skeletons composed of calcium carbonate; the minerals may include calcite and/or aragonite. These skeletons provide the characteristics used for recognising both living and fossil species that can be present in great abundance at their remains form limestones (Taylor and Weedon, 2000). The wide mineralogical spectrum of bryozoans makes them a good group for investigating the reduction of calcification in

carbonate produced marine organisms cased by oceanic acidification and increased seawater temperatures (Kuklinski and Taylor, 2009).

The use of an electron microscope is very important to study the microscopic crystallites which are the fundamental constituents of bryozoan skeletons. Microscopic examination of bryozoans is necessary for species identification. The skeletons of the zooids which make up bryozoan colonies provide most of the morphological characters used in the taxonomy of both fossil and recent species. These crystallites vary in shape, arrangement and crystallographic orientation. Several skeletal fabric types can be recognised, with individual walls often comprising a succession of these fabrics. Among cyclostome bryozoans, the calcitic skeleton is usually lamellar, consisting of tabular or lath-like crystallites stacked like tiles at a low angle to the wall surface. Cheilostome bryozoans may exhibit a similar ultrastructure but more commonly have fibrous skeletons consisting of needle-like or bladed crystallites oriented almost perpendicular to wall surfaces (Taylor and Weedon, 2000).

Each individual, or zooid, is enclosed in a sheath of tissue, the zooecium that in many species secretes a rigid skeleton of calcium carbonate. Each zooid has a single opening, the orifice. Through this opening, the lophophore, a ring of ciliated tentacles centred on the mouth, protrudes to capture small food particles (Figure 1.4). The lophophore can be retracted very rapidly by specialized retractor muscles, and the opening closed by the operculum as shown in Figure 1.5 (McKinney and Jackson, 1989). The mouth of the bryozoan opens into a U-shaped gut; the anus is located just outside the lophophore. From this arrangement comes the alternative name for the Bryozoa, the Ectoprocta. The body also contains a coelom and gonads; there is a small central ganglion, or brain, but there are no specialized excretory or respiratory systems in the bryozoans. The most common type of zooid is the feeding autozooid. A network of strands of mesothelium called the funiculus connects the mesothelium covering the gut with that lining the body wall. The mesothelium surrounds a space filled with fluid that enables autozooids to share food with each other and with any non-feeding heterozooids (Nielsen, 2001). Heterozooids are dependent on functioning autozooids for nutrients. Heterozooids are specialized for producing and brooding eggs. Avicularia are small heterozooids in which the zooecium and operculum form a beak-like, snapping structure that deters small predators. Vibracula bear long setae, or bristles, and are thought to function in cleaning the bryozoan colony, while kenozooids are small heterozooids that strengthen and support the colony as well as fill space. Bryozoan colonies show a range of integration. The most integrated colonies behave like individual organisms, for the zooids

making up the colony are all specialized for certain functions and connected to each other (McKinney and Jackson, 1989).

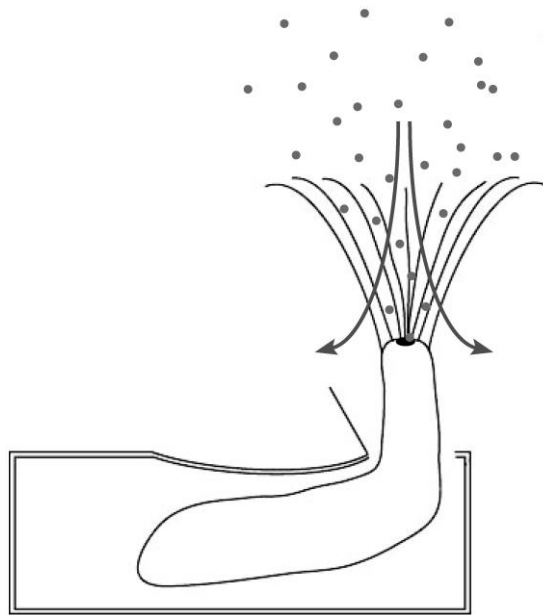


Figure 1.4: A diagram of a single bryozoan zooid in side view. The small circles represent food particles that are being drawn down through the lophophore toward the mouth, which is at the base of the lophophore. Arrows indicate the direction of water flow (Pratt, 2004).

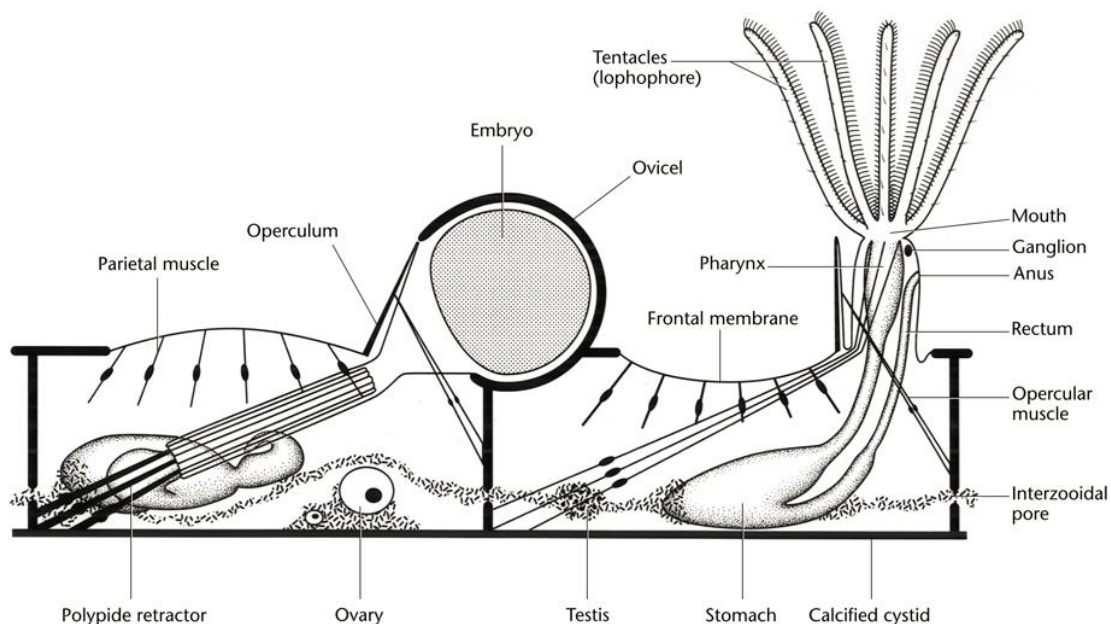


Figure 1.5: Diagram of two zooids in a cheilostome colony. The right zooid has protruded the polypide by contracting the parietal muscles, whereas the left zooid has retracted the polypide (Nielsen, 2001).

Bryozoans are considered to cause a nuisance in some situations. For example over 125 species are known to grow on the bottoms of ships, causing drag and reducing the efficiency

and manoeuvrability of the fouled ships. Moreover, bryozoans may foul pilings, piers, and docks and some freshwater species may form great jellylike colonies so huge they clog public or industrial water intakes. Nevertheless, bryozoans have this remarkable capability of producing a remarkable variety of chemical compounds (Sharp et al., 2007), some of which may find uses in medicine. The compound bryostatin 1 is produced by a marine bryozoan (*Bugula neritina*). Bryostatin has shown diverse biological effects including; anti-cancer properties (Barr, 2009; Jorgensen, 2005), anti-HIV properties (Mehla et al., 2010), activity against Alzheimer's disease, neural growth and repair, and the reversal of stroke damage (Lu et al., 2011).

In nature, Bryozoa increase local biodiversity on the seabed by offering shelter for other animals and acting as prey for limpets, small fish and sea urchins. Moreover, they feed on phytoplanktons that require carbon dioxide in order to grow and reproduce. The carbon in the phytoplankton is then taken by the bryozoans and used to form its skeleton and tissues (Barnes, 2011).

Bryozoans are ecologically important due to their feeding method as suspension feeders; they act as living filters in the marine environment therefore bryozoans keep the water clean because they are filtering out any extra food debris and acting as a sink for carbonate in the form of the produced skeletons. As filter feeders, bryozoans control phytoplankton populations in their environments. It has been reported that in a day a single zooid may filter 8.8 ml of water (Wright, 2016). Adult bryozoans use their tentacles to move food particles to their mouths. In some species, the ciliated tentacles of the lophophore are arranged in a horseshoe shape with food groove at the base of the lophophore, leading to the mouth. In other bryozoans the ciliated tentacles of the lophophore are arranged in a circular shape with each tentacle having one ciliated frontal tract and two ciliated lateral tracts. The cilia create a feeding current that flows toward the mouth, also directing larger particles toward the mouth by changing the direction of their stroking motions. These types of zooids also have a ciliated tract leading to the mouth, located inside the tentacle area of the lophophore. In some species, groups of zooids work together to create currents for feeding and waste removal (Brusca and Brusca, 2003; Buchsbaum et al., 1987; Ruppert et al., 2004). In contrast to other filter feeders such as sponges, bryozoans show huge tolerance to pollution. They can thrive especially well when situated downstream of sewage contamination and heavy agricultural runoff (Wright, 1997).

Bryozoans offer considerable advantages to the study of the effects of climate change in oceans. The skeleton of Bryozoa colonies is made of calcium carbonates and the decreased pH derived from ocean acidification causes corrosion, changes in mineralogy, and a decrease in the survivability of the colonies (Smith, 2014).

1.8.2. Polychaetes

Polychaetes, or bristle worms, are a very common and diverse class of worms with over 10,000 species. Polychaetes are marine worms, they are often brightly coloured and can be found in tubes and burrows in the sand and mud of the beach to the depths of the ocean or even just free living in the water. They all have bristles on their segmented bodies; Polychaetes come in an impressive range of sizes from just 1mm to 3m long (Nature, 2015). Polychaetes play a major role in the functioning of benthic communities, in terms of recycling, reworking and bioturbation of marine sediments and in the burial of organic matter (Hutchings, 1998). They are often the numerically dominant macro-benthic taxon in these sediments. Polychaetes may therefore be good indicators of species richness and community patterns in benthic invertebrate assemblages. The reason for this is not necessarily the high abundance of this taxon, but probably related to the high diversity of feeding modes within this group and their extraordinary ability to adapt to a whole range of habitats and environmental variation (Fauchald et al., 1979) Figure 1.6. Polychaetes are also well suited as indicators of environmental disturbance, since the group contains both sensitive and tolerant species and they are found along the whole gradient from pristine to heavily disturbed areas. The presence or absence of specific polychaetes in marine sediments provides an excellent indication of the condition or health of the benthic environment (Pocklington et al., 1992).



Figure1.6: Polychaete *Spirobranchus triqueter* feeding tentacle crown (Alchetron, 2017).

1.8.3. Barnacles

Barnacles are a type of arthropod related to crabs and lobsters. Barnacles are marine animals and tend to live in shallow and tidal waters. They are sessile suspension feeders that live inside shells, which are usually constructed of six plates (Doyle et al., 1997) Figure 1.7. Barnacles are often perceived to be major fouling agents, because they will grow abundantly on ships and in doing so disrupt the flow of water over the hull. Barnacles will also clog the pipes of power installations on the coast, and as a response to this widespread damage anti-fouling paints and other anti-fouling devices have been developed in the attempt to prevent barnacle growth.



Figure 1.7: Diagram of barnacle feeding appendages (Waterwereld, 2017).

1.9. Competitive interaction between epifaunal species

Marine invertebrate communities encrusting biogenic reefs provide a diverse habitat system for studying the relationships between sessile epifaunal species and their hosts (Sellheim et al., 2010). Competition for space is one of the most important processes that shapes the structure and succession of benthic communities (Khalamana and Lezin, 2015). Taylor (2016) reported two types of competitive interactions between sessile marine invertebrates on hard substrate: fouling and marginal. Fouling which is the result of a larva settling on the living surface of an established individual. Marginal encounters occur when two species share the same space and come into contact during their growth. These interactions may involve individuals of the same species (intra-specific) or different species (inter-specific). There are three outcomes in the inter-specific interaction: overgrowths, reciprocal and stand-off which are described in detail in chapter 3 of this thesis.

Sessile marine invertebrates can change their morphology in response to biotic signals from predators or competitors (Padilla, 1996), for example through the induction of spines in bryozoans, deformation to shell morphologies in barnacles and thicker shells in mobile gastropods (Gooley et al., 2010). Most solitary (polychaetes and barnacles) and colonial (bryozoans) animals differ in their ability to encrust space on hard substrata. However, colonial animals are superior space colonizers due to their unspecific growth which allows continuous occupation of space without the stages of sexual reproduction and recruitment (Jackson, 1977).

1.10. Disturbances effect on marine benthic communities

Mussel beds provide refuge to benthic communities from physical stress and predation (Lutz-Collins et al., 2009). *M. modiolus* clumps on muddy substrata are more fragile than larger aggregations. However, the damage caused by physical activities from towed fishing gear disrupts and flatten mussel clumps and larger aggregations, and reduces the habitat value (Holt et al., 1998; Cook et al., 2013). Natural disturbance within the reef, such as mussel growth, mortality, and movement from the clump may affect the resident epifaunal communities. However, the rapid colonization of opportunistic species could establish new competitor species that may cause severe changes in species composition and diversity (Lutz-Collins et al., 2009, González-Rivero et al., 2015). In addition disturbances may indirectly shift the structure and functioning of benthic communities by the partial or total removal of

dominant species and change the dominance structure (Herkul et al., 2011). Many ecosystems possess multiple opportunistic species and although many are relatively weak competitors, a competition between opportunistic species and the first colonizers could have a strong bearing on community dynamics (González-Rivero et al., 2015).

1.11. Reefs in Qatar

Pearl oyster *Pinctada radiata* (Leach, 1814) and coral reefs are the most diverse habitats in Qatar and the Arabian Gulf marine environment (Al-Ansi and AL-Khayat, 1999). In Qatar pearl oysters were exploited for natural pearls as its main economic resource that then declined with the development of cultured pearls in Japan during the 1930s (AL-Khayat and Al-Ansi, 2008). Al-Khayat and Al-Maslamani (2001) have contributed to the knowledge of fishing industry and pearl oyster beds associated fouling epifaunal species. However, bryozoan distributional abundance and community structure associated with pearl oyster and coral reefs remain unknown. The marine environment in the Arabian Gulf is characterised by extremes of temperature and salinity known to be experienced by coral reefs globally, sea surface temperatures in summer often exceeding 36 °C with Salinity observations as high as 45 EC (Sale et al., 2011; Feary et al, 2013; Burt et al., 2014). Investigating the conditions of coral reefs and associated epifaunal species community structure, population dynamics, and growth rate that exist in naturally extreme environments could be used to predict the role of climate change in the condition of coral reefs globally (Burt et al., 2014).

The overall aim of this study is to investigate the factors influencing biodiversity, abundance, spatial distribution and successional patterns of encrusting epifaunal communities in Biogenic habitats of the North- East Atlantic and Qatar. The Chapters will cover the following:

1. Chapter 2: species diversity and composition of horse mussel habitats are measured in relation to shell region and size.
2. Chapter 3: competitive interactions of bryozoan species on horse mussel shells are investigated in relation to shell region and size.
3. Chapter 4: biodiversity and mineralogy of Bryozoa species are documented from coastal waters of Qatar.
4. Chapter 5: study findings and future work.

2. Chapter 2: Investigation of the factors influencing the establishment and succession of North-East Atlantic epifaunal communities on *Modiolus modiolus* horse mussels from established biogenic reefs

2.1. Introduction

2.1.1. Horse mussel reefs and their conservation status

Horse mussels (*Modiolus modiolus*) can aggregate together to form biogenic reefs of scattered clumps and expansive beds that accumulate silt, organic rich sediment comprising faeces and pseudofaeces from the mussels, and shell debris. The result of this is production of raised beds, bound together by a matrix of byssus threads and shell (Rees, 2009). Horse mussels significantly modify the habitat providing hard substratum in sedimentary areas and a refuge and ecological niche for a wide variety of associated organisms (Lancaster et al., 2014). Horse mussels are filter feeders; they play a major role in improving water quality and controlling levels of phytoplankton blooms, thus influencing the dynamics of coastal systems diversity, as well as contributing significantly to nutrient fluxes from the benthos to the water column (Warwick et al., 1997).

Mussel reefs of *Modiolus modiolus* have been identified as biodiversity habitats that are supported under Marine Protected Areas (MPAs) through international and national legislation (Cook et al., 2013). The present study highlights the value of horse mussel habitats by measuring species diversity and community composition on horse mussel shells across sites in the North-East Atlantic. A greater understanding of the diverse and complex ecological services provided by horse mussel beds is needed in order to inform quality assessment. Water filtration is one of the key ecosystem services provided by horse mussel beds.

2.1.2. Horse mussel feeding

Horse mussels are efficient filter feeders capable of taking up phytoplankton from the water and accumulating nutrients, changing the concentration of these both in the sediments and in the water column (Soto and Mena, 1999). Horse mussels suck water in through the siphon for breathing and filtering to feed on plankton and other microscopic sea creatures which are free-floating in seawater. The pallial cavity contains a pair of very large gills that are used to capture food particles suspended in the inhalant water current. The food is bound in mucus

that is carried by cilia along food grooves on the edges of the gills to the mouth region. Here particles are sorted by the ciliated labial palps before they enter the mouth. The food then moves to the stomach, which is large and complex with sophisticated ciliary sorting mechanisms (Bunje, 2001).

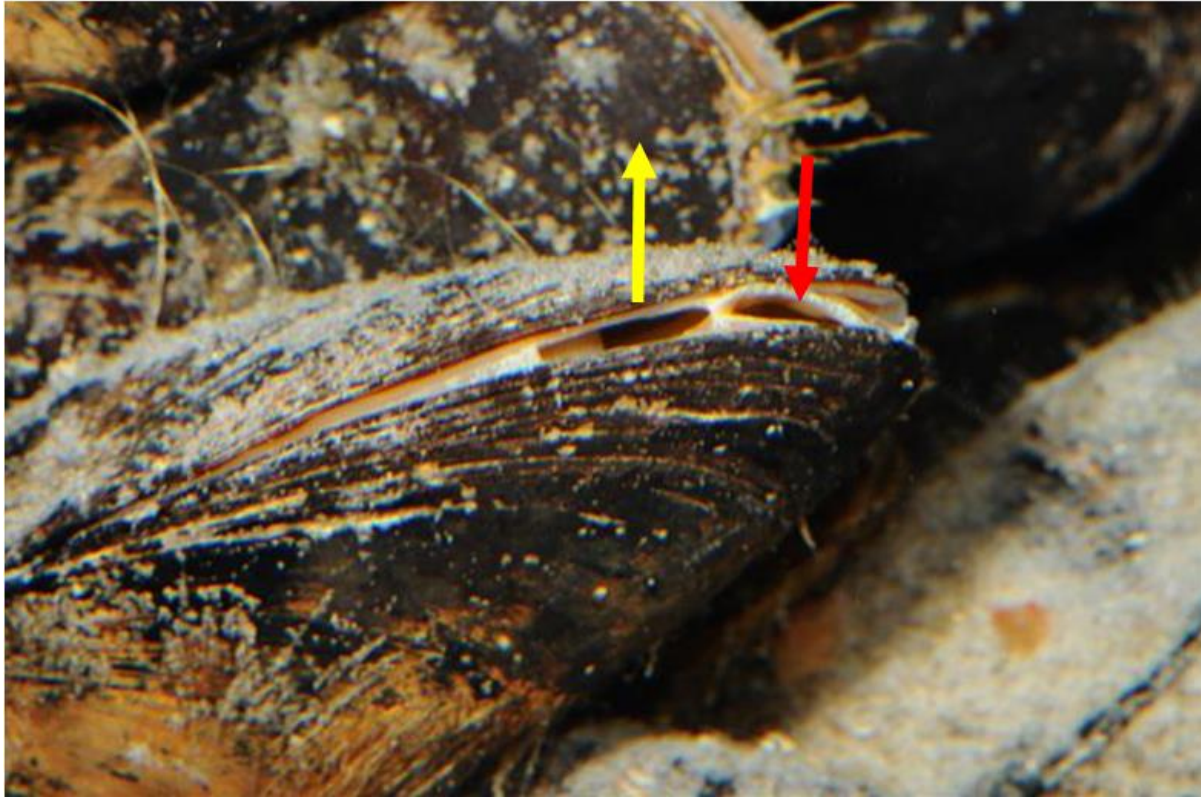


Figure 2.1: Filter feeding in horse mussel *M. modiolus*, seawater drawn in through the inhalant siphon as illustrated by the red arrow, the wastewater exits through the exhalant siphon as illustrated by the yellow arrow (*Modiolus modiolus*, 2017).

The distribution and concentrations of suspended particle size in the water vary with wave action and upwelling conditions. The distribution of particle sizes in the water column range from 0.5 μm to 125 μm in diameter (Stuart and Klumpp, 1984). Different suspension feeding invertebrates that occur in the same habitat, such as reef communities, fouling communities or kelp bed communities can take advantage by utilising particle selection for preferred sizes; this may result in competition for specific sized food particles in a turbid environment. For example most mussel species have been found to retain all particles greater than 4 μm , but smaller particles are retained with less efficiency, while several epifaunal species were found to retain very small particles less than 1.5 μm in diameter with the greatest efficiency. Particles released from sessile epifaunal species vary in size which may be subsequently available as a food source for the mussels, indicating that a mixed assemblage of epifaunal

species and mussels in biogenic reef may be able to utilize the suspended particles more efficiently than a single species population, due to recycling of the food particles.

2.1.3. Epifaunal communities

Space on the mussel surface is a factor which contributes to the epifaunal species community diversity, composition, and structure. The distribution of epifaunal species on horse mussels is most often established from a motile larval stage. The selectivity of the site of attachment by the larvae at the time of metamorphosis is important to adult species distributions. The majority of epifaunal species depend on motile larvae for dispersal. Larvae can remain in the plankton for a few hours to a few weeks, after which they metamorphose and attach to a substratum. A variety of physical factors can influence the settlement and attachment of epifaunal larvae such as light, temperature, water currents, and the texture and angle of the substratum surface as well as biological interactions within and between species that are important to determine which colonial species can occur in a particular area, which might cause the substratum to become monopolized by a single species or a small group of dominant species (Osman, 1977). Substrate sizes also affect the composition and structure of the epifaunal community. Preston (1962) hypothesised that a larger substratum will harbour a larger number of individuals and species of the settling larvae. Studies indicate that a linear relationship exists between the size of the substratum and the number of species of associated substrata (Sepulveda et al., 2003). Tsuchiya and Nishihira (1986) investigated the effect of blue mussel *Mytilus edulis* patch different in age and size on the associated epifaunal community structure. They reported that species composition in patches of young mussels differed from that of the patches of larger ones; this could be due to the short period of colonization for space in young mussels therefore less competition between the epifaunal species. While studies have been conducted on various shellfish species and for other types of biogenic habitat such as coral reefs, there is as yet no data for temperate, long-lived, biogenic reef building species such as horse mussels.

2.2.Aim and objectives

The aim of this study is to investigate the factors influencing biodiversity, abundance, spatial distribution and successional patterns of encrusting epifaunal communities.

Horse mussel epifauna was analysed from eight reef sites throughout the North-East Atlantic distribution range. The objectives of the study are:

1. To identify and quantify epifauna to species level on four regions of horse mussel shells to elucidate whether some regions of the shell are more important for diversity of epifauna than others.
2. To analyse the relationship between epifaunal abundance and species richness to mussel shell length, to understand how shell size influences the successional development of the epifaunal community.
3. Analyse biodiversity and abundance patterns of horse mussel epifaunal data using PRIMER v7 software and understand the relationship between the community to environmental and biogeographical factors.

2.3. Material and methods

2.3.1. Fieldwork

Samples of living horse mussels (*Modiolus modiolus*) were collected from eight horse mussel beds, located in the North-East Atlantic as shown in Figure 2.2. Details for each site are provided in (Table 2.1). Fifty living horse mussels were collected from each site. Samples were collected by members of the Heriot Watt University scientific diving team, using SCUBA equipment. Samples were kept in cooler boxes and transported as quickly as possible back to the laboratory for processing.

Table 2.1: Location information for North-East Atlantic horse mussel sample sites.

Site	Location	Position	Date	Maximum Depth
1	Ramsey Bay, Isle of Man	54° 21' 00 "N, 4° 18' 00 "W	24-9-2014	20m
2	Karlsruhe wreck, Orkney, Scotland	58° 54' 0" N, 3° 3' 0" W	2-4-2015	25m
3	Skarnsundet West Bridge, Norway	63°50'35.42"N, 11°4'31.54"E	8-7-2014	22m
4	North Llŷn Wales	52° 54' 33" N, 4° 27' 41" W	28-5-2015	22.5m
5	Port Appin, Scotland	56° 33' 38.2" N, 5° 21' 26" W	18-1-2016	25m
6	Loch Creran, Scotland	56°31'38.8"N, 5°20'21.2"W	19-1-2016	13m
7	Noss Head, Scotland	58° 28' 44.4" N, 3° 3' 3.24" W	13-6-2016	45m
8	Dornoch Firth, Scotland	57° 51' 0" N, 4° 3' 0" W	3-7-2016	11m

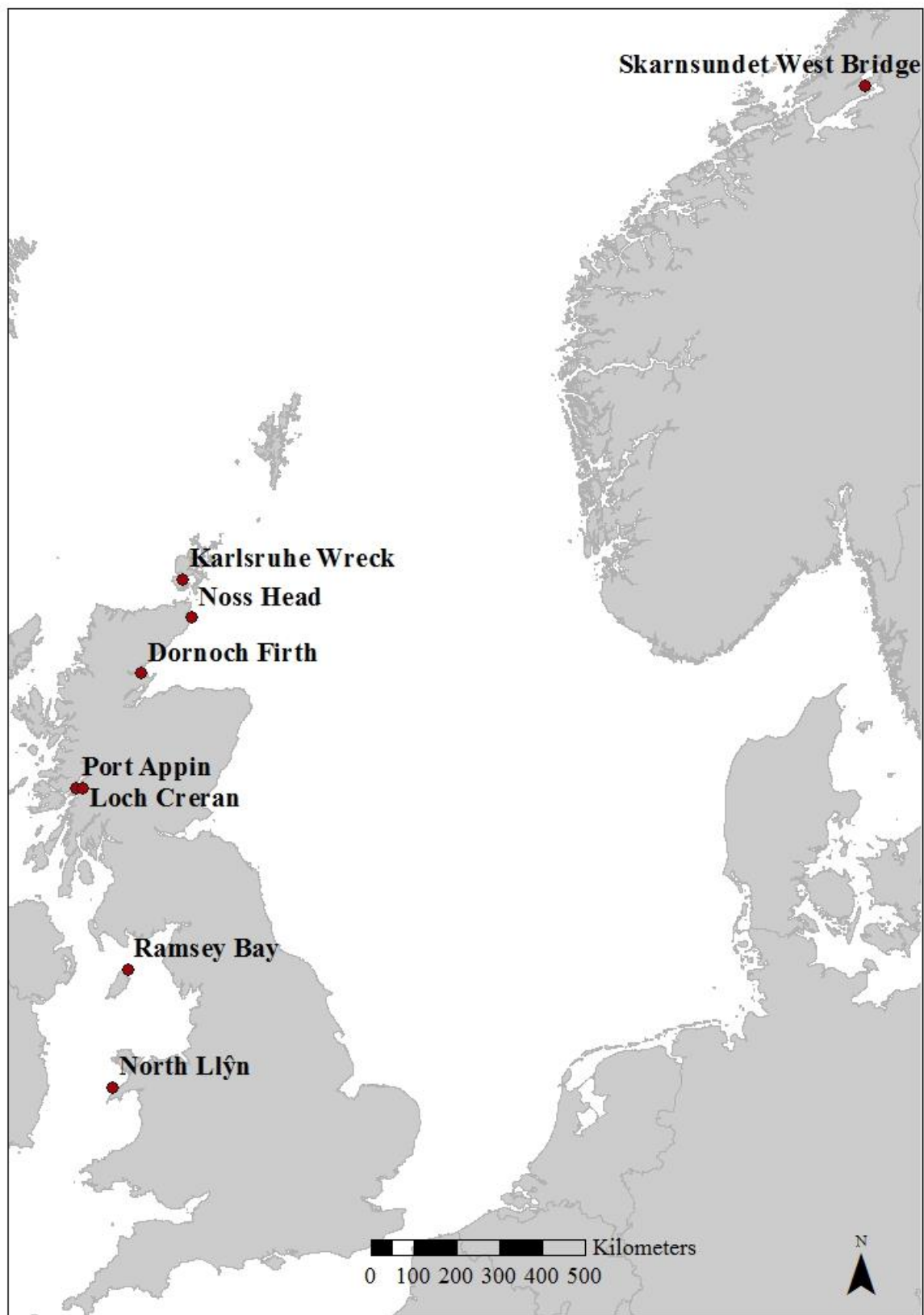


Figure 2.2: Map of sites in the North-East Atlantic where horse mussels were sampled from beds.

2.3.2. Sample processing

Horse mussel shells were opened and cleaned of soft tissue, rinsed in freshwater to get the salt off and then air dried overnight. The inner sides of all horse mussel samples were marked with the site (Ramsey Bay, Isle of Man: IOM, Karlsruhe wreck, Orkney: ORK, Skarnsundet West Bridge, Norway: NOR, North Llŷn: NW, Port Appin: PA, Loch Creran: LC, Noss Head: NH and Dornoch Firth: DOR), valve orientation (left or right valve), and shell region (1-4: Figure 2.3). In order to understand which regions of the outer shell were more successful in supporting epifaunal colonisation, the left and right valves of each specimen were analysed as four sections. The shell was divided in order to produce four equal shell regions for analysis. Posterior regions were distinguished from anterior regions using 3 mid points (A, B & C: Figure 2.3). Right valve sections were referred to as R1, R2, R3, and R4 and left as L1, L2, L3 and L4, (Figure 2.3). Using the pre-labelled shell regions, the epifaunal coverage of each species within each region was calculated and recorded in relation to: valve orientation (left/right), shell region (1-4) and shell length in mm.

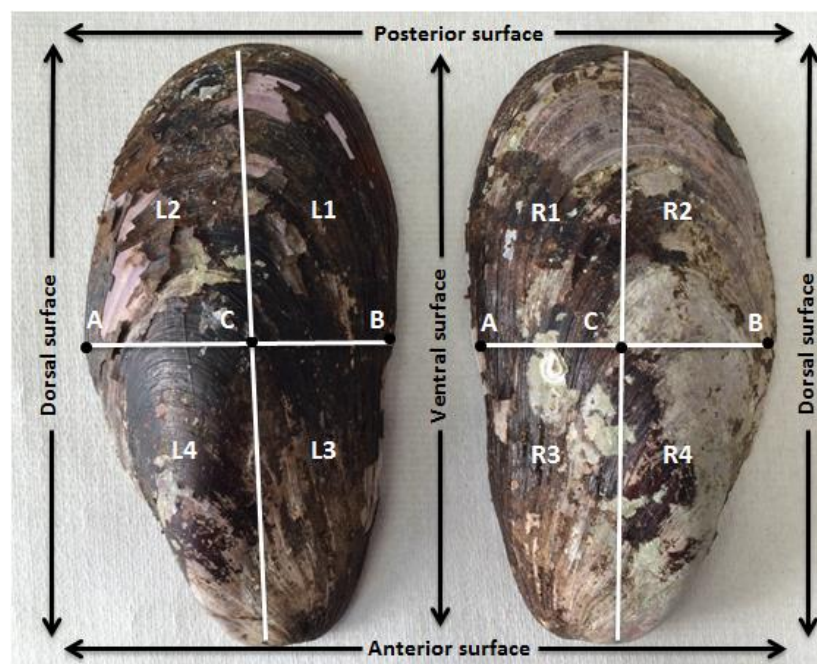


Figure 2.3: Methods used for defining horse mussel shell regions equally. A is equidistant over the total length of the dorsal surface. C is equidistant over the total length of each valve. B is equidistant between the umbo and the highest posterior point. L and R refer to left and right valve.

2.3.3. Identification and quantification of shell epifauna

A Leica MZ7.5 high-performance stereomicroscope was used to examine the horse mussel epifauna (bryozoans, polychaete and barnacles). British and European marine invertebrate identification key were used for species identification (Hayward and Ryland; 1995, 1998, 1999; Southward; 2008). Identifications and abundance counts were recorded into an excel spreadsheet for statistical analysis. For confirmation of species identification some of the dominant bryozoan species (*Patinella verrucaria*, *Chorizopora brongniartii*, *Escharella immersa*, *Reptadeonella violacea*, *Microporella ciliata*, and *Fenestrulina malusii*) from the Isle of Man site were imaged using the LEO 1455 VP SEM electron microscope in the EMMA Unit of the Natural History Museum London. Prior to scanning the bryozoan colonies were treated with 5 % domestic bleach solution for 1 hour then rinsed with water to remove any organic materials on the surface of the colonies and ensure that significant identification features were not obscured by contamination. Image J software was used to take multiple measurements of zooid characteristics (zooid length, width, orifice size, avicularia and ovicells) in order to confirm species identification (Appendix K).

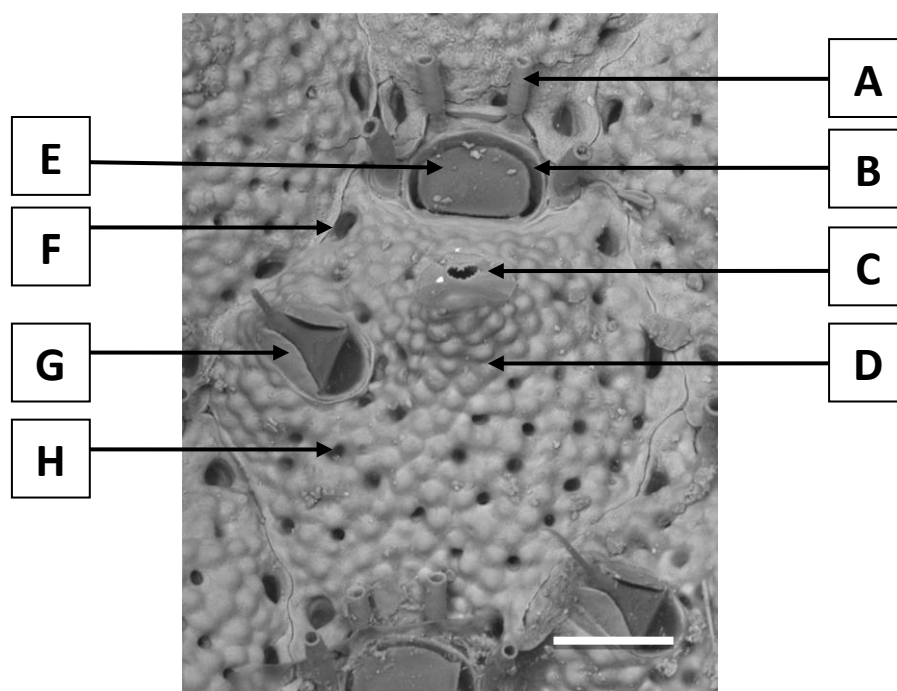


Figure 2.4: characteristic features of *Microporella ciliata* from Isle of Man (scale bar= 100 μ m). A: spine, B: orifice, C: ascopore, D: frontal shield, E: operculum, F: marginal pore, G: avicularia, H: frontal shield pore.

2.3.4. Data processing and statistical analysis

Data relating to shell regions was merged from both valves, so that the contribution from both shell valves was used in the statistical analysis (Figure 2.3). In a subsequent analysis R1 and R2 as well as R3 and R4 were merged into anterior-posterior regions to increase the number of colonies in each comparison. Epifaunal differences in shell size and shell region were tested across the sites. Shells were grouped into size classes. Differences in epifaunal diversity and abundance between shell sizes were statistically tested. Size classes were tested from the 400 horse mussels across all sites. Size classes consisted of 4 to 8 replicates (Appendix B). Diversity indices were calculated using epifaunal community data to give an understanding of the overall community complexity of horse mussel shell epifauna. Total species (S), total individuals (N), Species richness (d), Pielou's evenness (J), Shannon Wiener diversity (H [Loge]) and Simpson's diversity (1-Lambda) were calculated.

Multivariate analyses were conducted using the software PRIMER v7 (Clarke and Gorley, 2015). Data was initially square root transformed in the cluster analysis to limit the influence of species showing high numerical abundance that varied by one order of magnitude. A Bray-Curtis similarity matrix was calculated to quantify the compositional dissimilarity between the samples at each site. A SIMPROF analysis was conducted on the epifaunal data to test the hypothesis that within the set of sites there is no genuine evidence of multivariate structure (Clarke and Gorley, 2015). An analysis of similarities (ANOSIM) test is a re-sampling technique that uses permutation/randomization methods on Bray Curtis similarity matrices to identify differences among groups of samples. ANOSIM analyses of similarity (9999 permutations), were used to test for community differences between different shell regions and between shell size classes. SIMPER was used to describe the compositional dissimilarity between horse mussel shell regions and size classes. The following hypotheses were tested:

1. The epifaunal community on the anterior part of the horse mussels shell not significantly different to the posterior.
2. Filter feeding in the posterior region of horse mussels will not affect the diversity of epifaunal communities on the shell.
3. Current flow will not increase the diversity of epifaunal species on the posterior regions of the horse mussels shell.
4. There is no significant difference in epifaunal abundance with an increase in shell size of horse mussels.

2.4.Results

2.4.1. Imaging of epifauna for identifications

Species identifications were conducted using either light microscopy or where required, Scanning Electron Microscopy (SEM). Selections of the key species identified are illustrated in Figures 2.5-2.11.

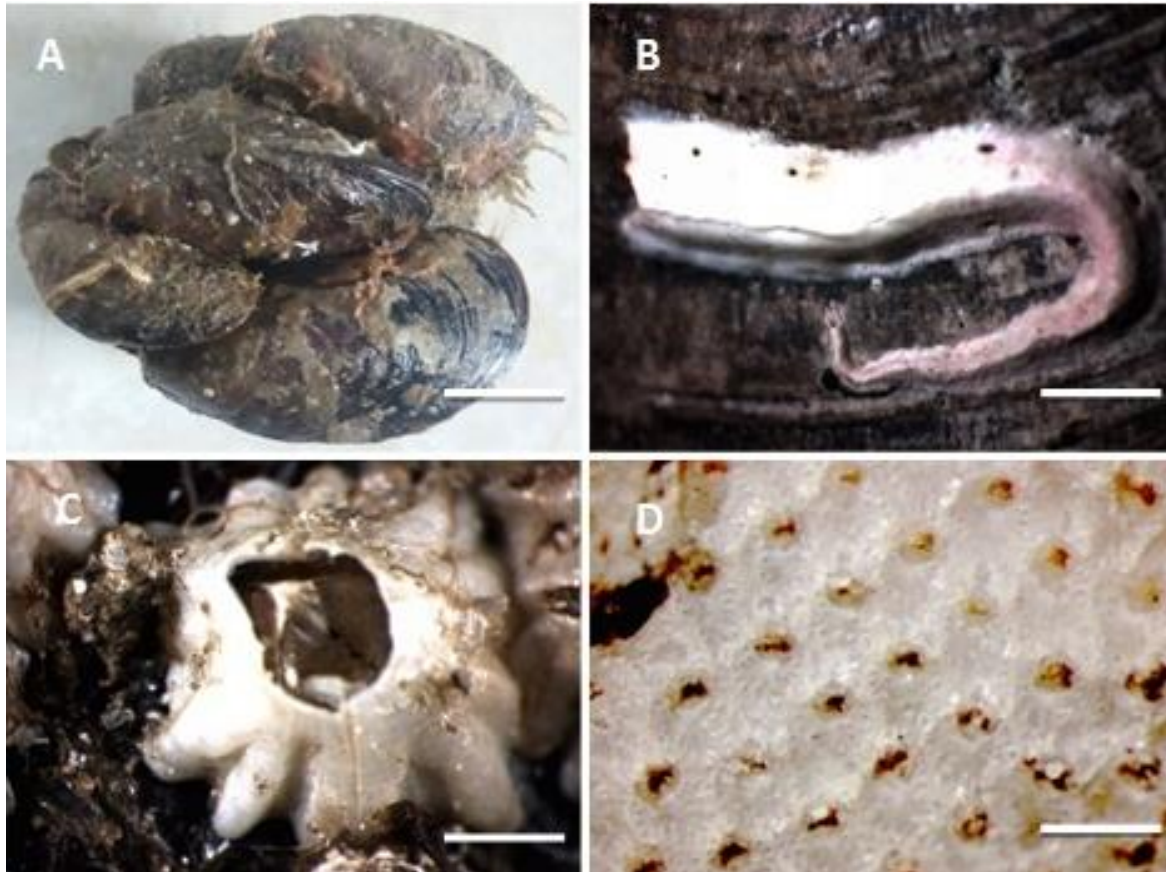


Figure 2.5: A: Horse mussel clump structure at Noss Head, Scotland (scale bar= 5 cm), B: *Spirobranchus triqueter* from Skarnsundet West Bridge, Norway (scale bar= 2 cm); C: *Balanus balanus* from Dornoch Firth, Scotland, scale (bar= 2 cm); D: Light microscope picture of *Escharella immersa* from Ramsey Bay, Isle of Man, Irish Sea (scale bar= 1 cm).

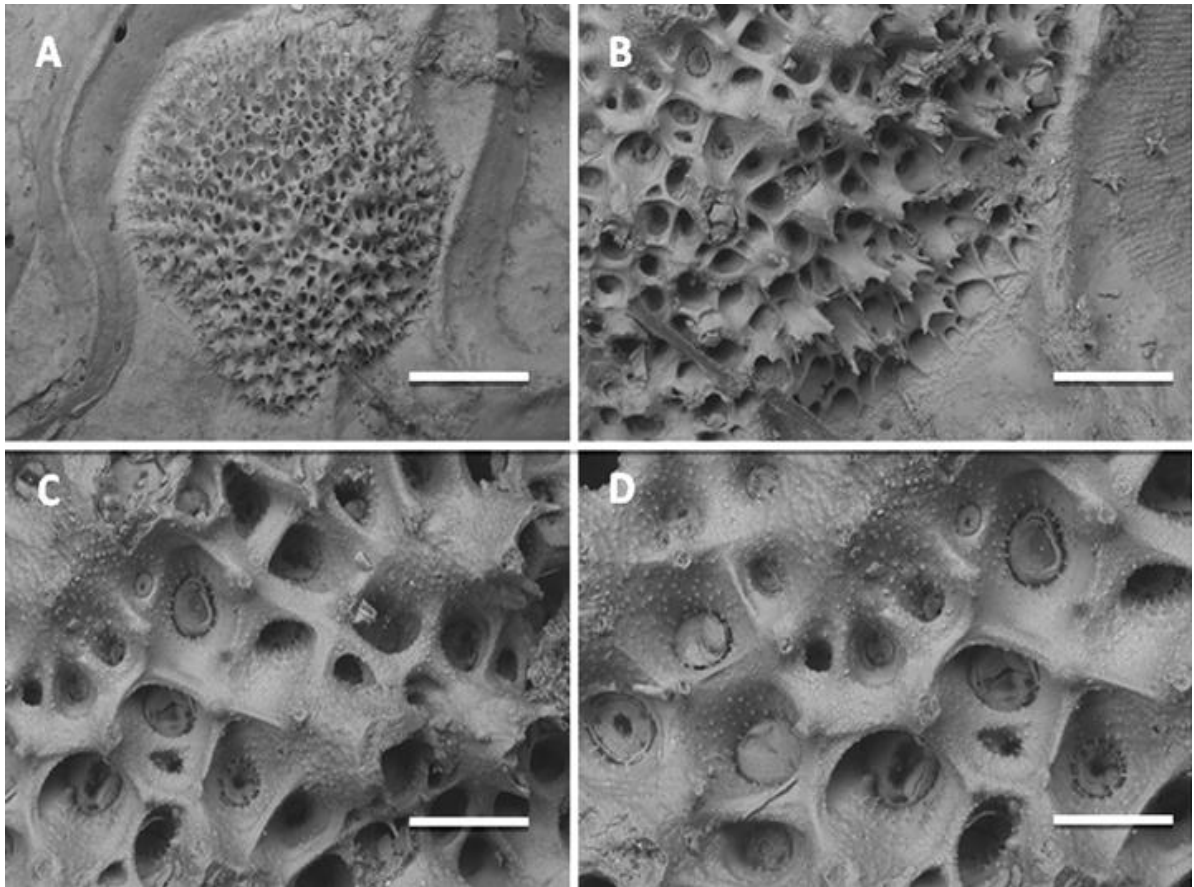


Figure 2.6: Scanning electron micrographs of *Patinella verrucaria* from Isle of Man. A: *Patinella verrucaria* colony (scale bar= 200 µm), B: close-up of colony calcified tubes edge (scale bar= 200 µm), C: close-up of zooids orifice (scale bar= 100 µm), D: extra close-up of zooids orifice (scale bar= 20 µm).

Order *Cyclostomatida* Busk, 1852

Suborder *Rectangulata*

Family *Lichenoporidae* Smitt, 1867

Genus *Patinella* Gray, 1848

Patinella verrucaria (Linnaeus, 1758)

Lichenopora verrucaria – Hayward & Ryland, 1995: p. 640, Fig. 11.3.

Material

Isle of Man: sample collected offshore from horse mussel bed, found encrusting on *Modiolus modiolus* shell substrata.

Description

Colony is discoid. Zooids disposed around a small central area, the orifices raised, with a single pointed process. Central alveolae with thin walls sometimes roofed over. Opening of brood chamber is on an upright flaring tube.

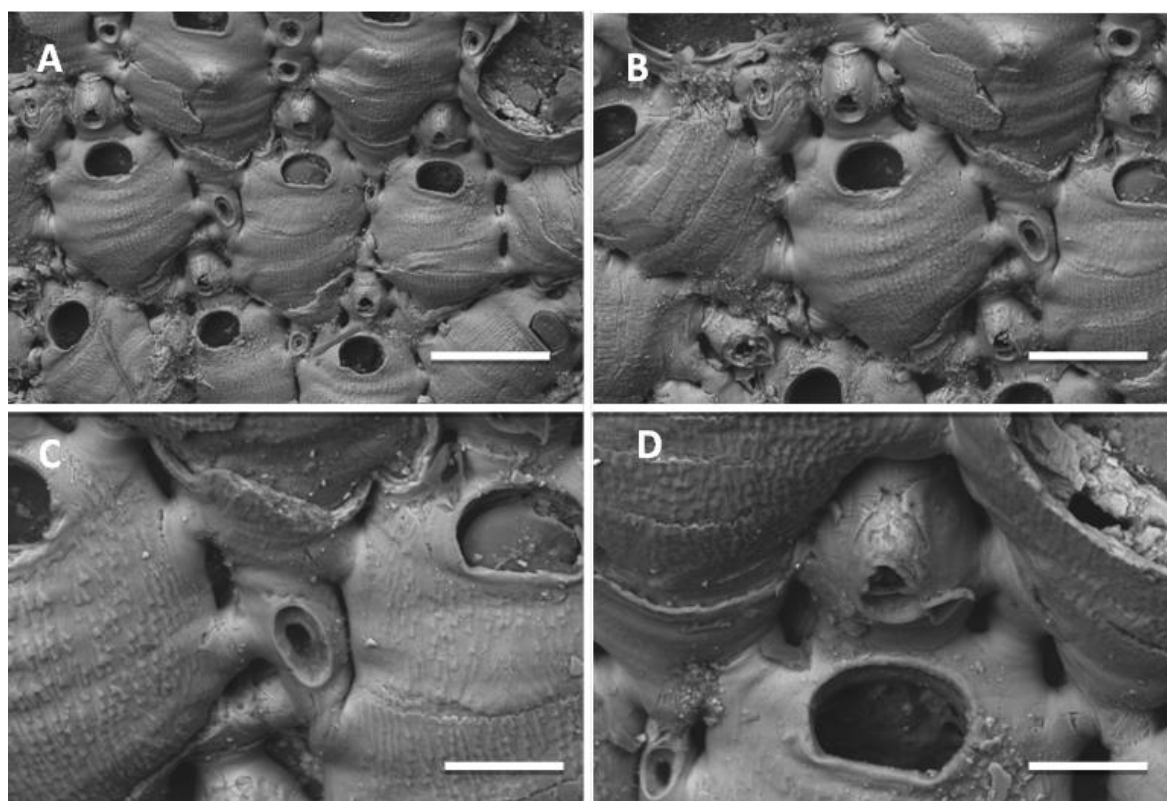


Figure 2.7: Scanning electron micrographs of *Chorisopora brongniartii* from Isle of Man. A: close-up of a group of zooids (scale bar= 100 µm), B: close-up of a single zooid orifice, operculum, kenozooids and avicularium (scale bar= 20 µm), C: close-up of kenozooid (scale bar= 20 µm), D: close-up of avicularium (scale bar= 10 µm).

Order *Cheilostomatida* Busk, 1852

Suborder *Flustrina* Smitt, 1868

Family *Chorisoporidae* Vigneaux, 1949

Genus *Chorisopora* Hincks, 1879

Chorisopora brongniartii (Audouin, 1826)

Flustra brongniartii – Audouin, 1826: p. 240, pl. 10, Fig. 6.

Chorizopora brongniartii –Hincks, 1880: p. 224, pl. 32, Figs. 1-4; Hayward & Ryland, 1999: p. 100- 101, Figs. 24C, D; 25.

Material

Isle of Man: sample collected offshore from horse mussel bed, found encrusting on *Modiolus modiolus* shell substrata.

Description

Colonies form broad spreading sheets, thin and translucent. Autozooids are oval, occasionally pear-shaped or irregular, separated by shallow grooves. Adjacent autozooids linked by short tubules, extensions of the pore chambers. Frontal wall fine grained marked with ridges. Orifice wider than long, semicircular, subterminal, with thin rim no peristome. Avicularia vicarious; cystid small, linked to adjacent autozoid by communication tubes, mandible at an acute angle to the frontal plane, triangular, directed distally. A single avicularium situated distal to each zoid. Small irregularly shaped kenozooids, linked by tubules to surrounding autozooids; generally small with circular or oval orifice but no operculum. Ovicell not observed in the material collected here.

Table 2.2: Characteristics measurements of *Chorizopora brongniartii* species from Ramsey Bay, Isle of Man site.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	262.6 \pm 26.9	190.2 – 308.2	22
Autozoid width	181.5 \pm 27.8	115.9 – 238.4	22
Orifice length	47.4 \pm 5.2	35.8 – 55.9	17
Orifice width	63.9 \pm 11.1	45 – 87.3	17
Avicularium length	87.3 \pm 13.4	67.4 – 118.8	15
Avicularium width	70.1 \pm 14.1	48.7 – 89.8	15
kenozooids length	70.5 \pm 24.8	50.6 – 128.1	11
kenozooids width	51 \pm 18.1	22.9 – 80.2	11

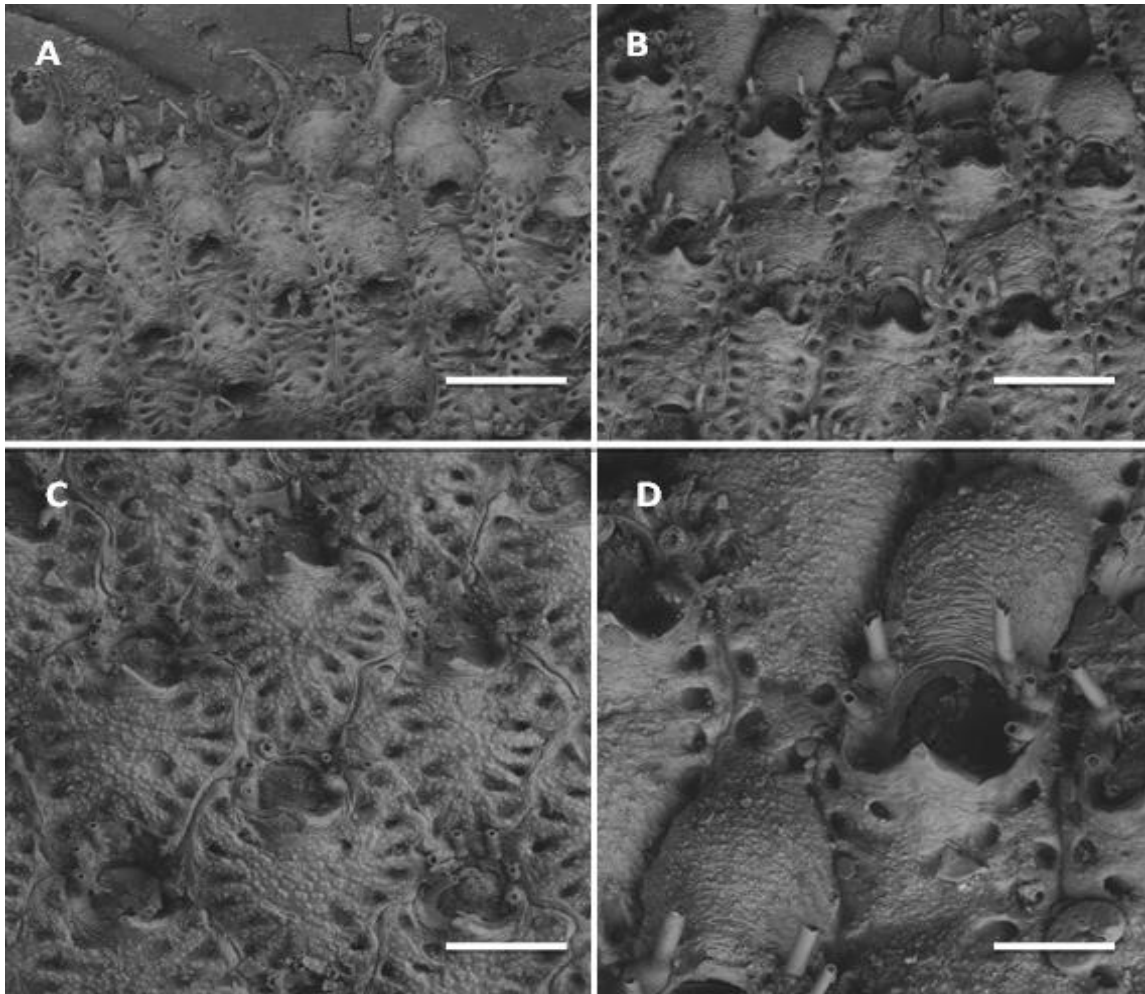


Figure 2.8: Scanning electron micrographs of *Escharella immersa* from Isle of Man. A: *Escharella immersa* growing edge of the colony (scale bar= 300 µm), B: close-up of an ovicellate group of zooids (scale bar= 200 µm), C: close-up of zooids orifice, spines (scale bar= 100 µm), D: extra close-up of zooids peristome and ovicell (scale bar= 100 µm).

Family *Romancheinidae* Jullien, 1888

Genus *Escharella* Gray, 1848

Escharella immersa (Fleming, 1828)

Lepralia immersa – Fleming, 1828:533.

Mucronella peahii – Hincks, 1880: 360, pl. 50, Figs 1-5.

Escharella immersa – Hayward & Ryland, 1999: p. 122- 123, Figs. 35, 37A.

Material

Isle of Man: sample collected offshore from horse mussel bed, found encrusting on *Modiolus modiolus* shell substrata.

Description

Colony grows as an extensive unilaminar sheet. The autozooids are oval to hexagonal, becoming irregular in outline, convex, separated by distinct grooves. The frontal wall is finely granular, areolae small, accentuated by increasing calcification and becoming very marked, with stout interareolar ridges. The primary orifice is orbicular, with a broad, anvil-shaped lyrula, often with a concave distal edge, blunt, lateral condyles present. Six oral spines, Peristome well developed, thickened, with a stout, pointed proximally. The ovicell is broader than long, granular, recumbent on succeeding autozooids and immersed in secondary calcification.

Table 2.3: Characteristics measurements of *Escharella immersa* species from Ramsey Bay, Isle of Man site.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	473.2 \pm 22.2	442.1 – 517.1	15
Autozoid width	268.6 \pm 48.2	206.4 – 353.1	15
Orifice length	67.3 \pm 5.5	55.4 – 76.2	15
Orifice width	79.3 \pm 7.6	68.6 – 91.7	15
Ovicell length	190.5 \pm 20.7	165.8 – 220.4	7
Ovicell width	214.1 \pm 32.5	158.3 – 246.3	7

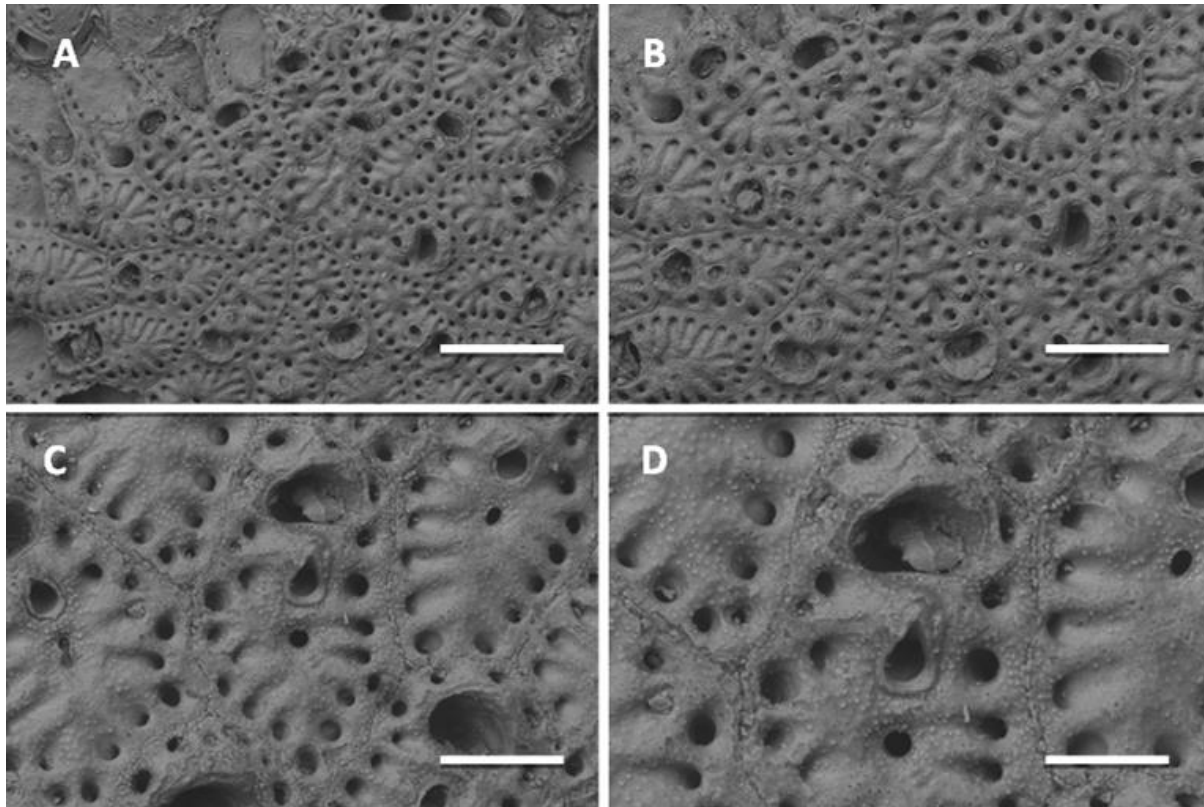


Figure 2.9: Scanning electron micrographs of *Reptadeonella violacea* from Isle of Man. A: close-up of the six ancestrula zooids (scale bar= 100 µm), B: close-up of ancestrula zooids (scale bar= 100 µm), C: close-up of autozooids orifice, basal pore-chambers, spiramen, and avicularium (scale bar= 100 µm); D: close-up of spiramen, and avicularium (scale bar= 20 µm).

Family *Adeonidae* Busk, 1884

Genus *Reptadeonella* Busk, 1884

Reptadeonella violacea (Johnston, 1847)

Lepralia violacea –Johnston, 1847: p. 325, pl. 57, Fig. 9.

Microporella violacea –Hincks, 1880: p. 216, pl. 30, Figs. 1, 2, 4.

Reptadeonella violacea – Hayward & Ryland, 1999: p. 186- 187, Figs. 70A, B; 71.

Material

Isle of Man: sample collected offshore from horse mussel bed, found encrusting on *Modiolus modiolus* shell substrata.

Description

Colonies form broad, often extensive, incrustations, deep purple when living, with paler edge of developing autozooids. Autozooids hexagonal, pyriform or lozenge shaped, flat or slightly concave with marked central depressions. The frontal wall is finely granular with a series of closely spaced marginal pores; a single round spiramen present in the central depression. Primary orifice semicircular; secondary orifice surmounting a short peristome, arched distally; a short triangular avicularium set on the sloping proximal side, directed distally or transversely. Numerous small basal pore-chambers present 14-16 in the distal half of each autozoid, each with a single communication pore. Larva metamorphoses to form six, symmetrically grouped, ancestrular autozooids.

Table 2.4: Characteristics measurements of *Reptadeonella violacea* species from Ramsey Bay, Isle of Man site.

Measurements	Mean \pm SD (μm)	Range (μm)	Zoids Number
Autozoid length	293.1 \pm 24.7	261 – 332.5	18
Autozoid width	187 \pm 15.9	161.1 – 223	18
Orifice length	41.4 \pm 6	31.8 – 50.9	15
Orifice width	62.3 \pm 5.8	52.3 – 72.3	15
Avicularium length	44.7 \pm 6.3	29.8 – 56.7	18
Avicularium width	33.1 \pm 3	26.1 – 38.9	18

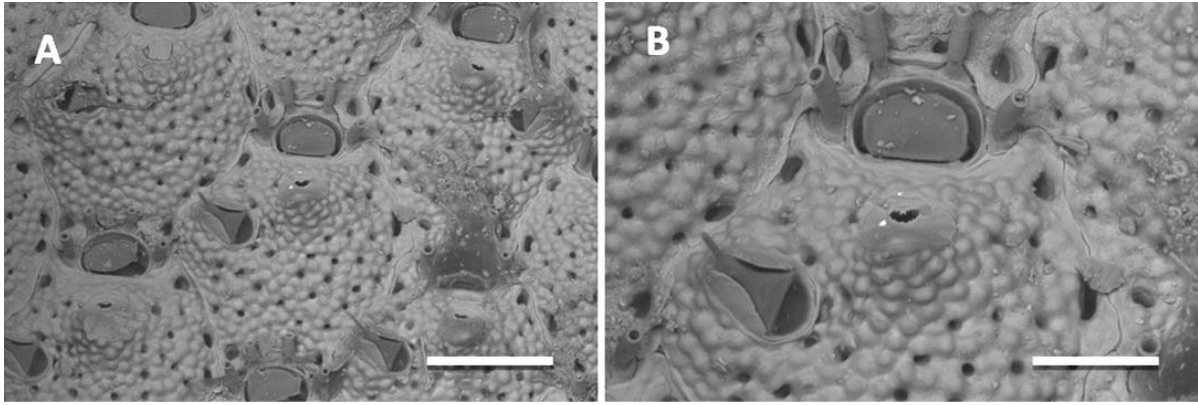


Figure 2.10: Scanning electron micrographs of *Microporella ciliata* from Isle of Man. A: close-up of a group of zooids (scale bar= 100 µm), B: close-up of a single zooid orifice, operculum, avicularium, oral spines and crescent shaped ascopore (scale bar= 20 µm).

Family *Microporellidae* Hincks, 1879

Genus *Microporella* Hincks, 1877

Microporella ciliata (Pallas, 1766)

Eschara ciliata –Pallas, 1766: p. 38.

Microporella ciliata – Hincks, 1880: p. 206, pl. 28, Figs. 1-5, 7-8; Hayward & Ryland, 1995: p. 653, Fig. 11.8; Hayward & Ryland, 1999: p. 296- 297, Figs. 134C, D; 136.

Material

Isle of Man: sample collected offshore from horse mussel bed found encrusting on *Modiolus modiolus* shell substrata.

Description

The colony is encrusting and silvery. The autozooids are oval to hexagonal, convex and separated by deep grooves. Frontal shield thick, coarse grained, perforated by numerous pores. The primary orifice is semicircular, with straight proximal border; four erect, pointed spines around the distal and lateral borders. The ascopore is large and crescentic; located on the distal face of a small umbo. The avicularia is single, lateral or proximal to the ascopore, on the right or left; rostrum short, triangular, acute to the frontal plane of autozooid, supporting a short setiform mandible, directed laterally or disto-laterally.

Table 2.5: Characteristics measurements of *Microporella ciliata* species from Ramsey Bay, Isle of Man site.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	570.4 \pm 24.1	527.6 – 603.9	7
Autozoid width	511.6 \pm 34.1	464 – 554.8	7
Orifice length	79.9 \pm 10.1	66.5 – 93.9	9
Orifice width	135.1 \pm 9.8	123.9 – 154	9
Avicularium length	127.6 \pm 15.5	101.2 – 148.1	10
Avicularium width	79.7 \pm 4.2	72.4 – 84.5	10
Ascopore length	37.2 \pm 9.2	25.3 – 52.9	7
Ascopore width	59.3 \pm 9.3	44.2 – 75.6	7
Mandible length	157.4 \pm 33.73	117.6 – 207.5	5
Mandible width	37.6 \pm 3.2	29.8 – 38.4	5

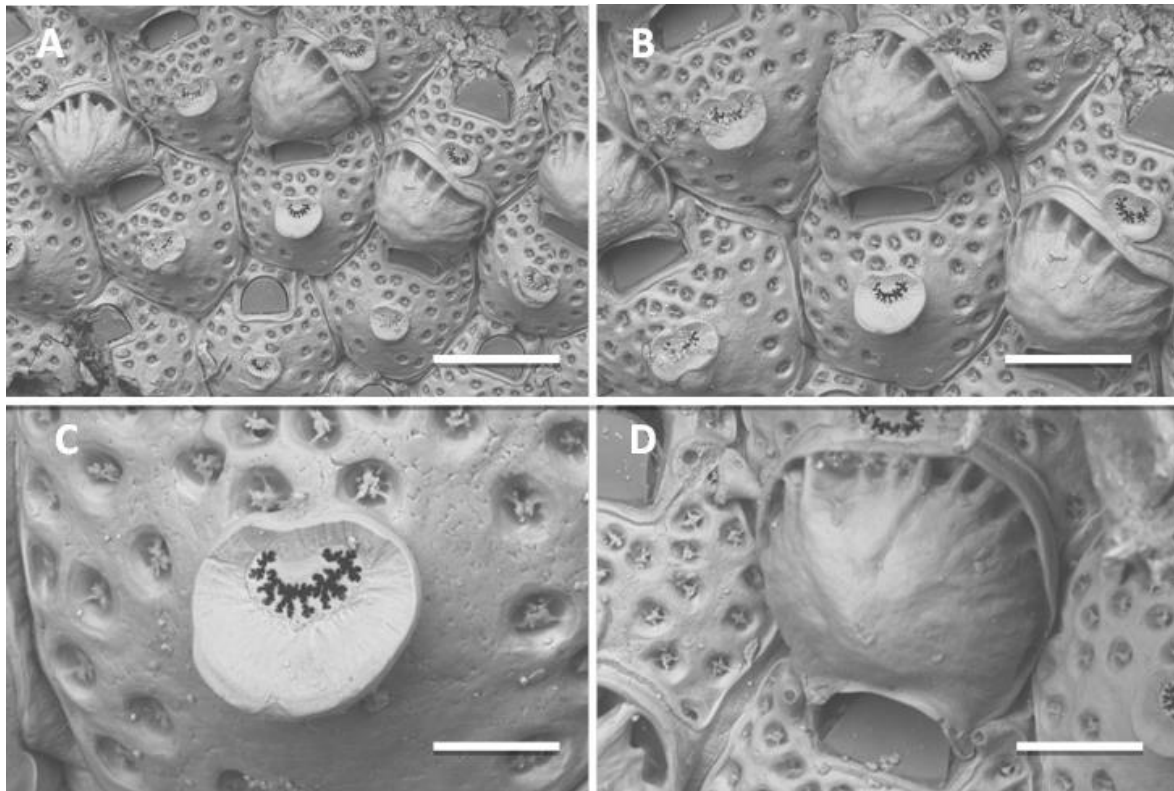


Figure 2.11: Scanning electron micrographs of *Fenestrulina malusii* from Isle of Man. A: close-up of a group of zooids (scale bar= 100 µm), B: close-up of a group of zooid orifice, operculum, oral spines, ovicell and ascopore (scale bar= 100 µm), C: close-up of ascopore (scale bar= 20 µm), D: close-up of ovicell (scale bar= 20 µm).

Genus *Fenestrulina* Jullien, 1888

Fenestrulina malusii (Audouin, 1826)

Cellepora malusii—Audouin, 1826: p. 239, pl. 8, Fig. 8.

Fenestrulina malusii – Hayward & Ryland, 1995: p. 653, Fig. 11.8; Hayward & Ryland, 1999: p. 300- 301, Figs. 137; 138A, B.

Material

Isle of Man: sample collected offshore from horse mussel bed, found encrusting on *Modiolus modiolus* shell substrata.

Description

Colonies forming white patches, Autozooids oval. The frontal wall is convex, smooth, punctate; with a number of round pores between the ascopore and the orifice. The orifice is semicircular, proximal edge straight, with a thin rim. Operculum pale brown with distinct

marginal sclerite. The orifice has two or three short distal oral spines. Ascopore broad, crescentic, inner rim with small denticulations; proximal edge raised and thickened. The ovicell is prominent, subglobular and recumbent on the distally succeeding autozoid, with a distal series of alternating ribs and spaces.

Table 2.6: Characteristics measurements of *Fenestrulina malusii* species from Ramsey Bay, Isle of Man site.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	422.1 \pm 55.4	330.9 – 499.7	10
Autozoid width	392.3 \pm 39.9	334.4 – 463.3	10
Orifice length	90.3 \pm 19.5	58.9 – 121.1	11
Orifice width	134 \pm 22.5	92.4 – 169.2	11
Ovicell length	253.5 \pm 32.7	197.1 – 295.3	8
Ovicell width	296.3 \pm 18.2	270.6 – 321	8
Ascopore length	76.9 \pm 13.8	48.3 – 103.1	12
Ascopore width	108.8 \pm 13.5	73.9 – 126.1	12

2.4.2. Species identification and biodiversity

Four hundred individual *Modiolus modiolus* were sampled in the present study, from eight sites across 36 degrees of latitude. Overall, 11 Stenolaemata and 36 Gymnolaemata bryozoans, four polychaete and three barnacle species were recorded (Table 2.7). The North Llŷn site had the highest number of species (n = 31). The site with the fewest species was Loch Creran (n = 4).

Table 2.7: Invertebrate species colonising horse mussel samples (n = 400) from North Llŷn to Norway. IOM: Ramsey Bay, Isle of Man; ORK: Karlsruhe wreck, Orkney, NOR: Skarnsundet West Bridge, Norway; NW: North Llŷn; PA: Port Appin, LC: Loch Creran; NH: Noss Head; DOR: Dornoch Firth.

Species	IOM	ORK	NOR	NW	PA	LC	NH	DOR
Phylum: Annelida								
Class: Polychaeta								
<i>Spirobranchus lamarckii</i>			✓		✓		✓	
<i>Spirobranchus triqueter</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Serpula</i> sp.			✓	✓	✓		✓	
<i>Spirorbis tridentatus</i>	✓	✓	✓	✓	✓		✓	
Phylum: Arthropoda								
Infraclass: Cirripedia								
<i>Balanus balanus</i>		✓	✓	✓	✓		✓	✓
<i>Balanus crenatus</i>					✓			✓
<i>Verruca stroemia</i>				✓	✓		✓	✓
Phylum: Bryozoa								
Class: Stenolaemata								
Order: Cyclostomatida								
<i>Crisia eburnea</i>	✓			✓	✓			
<i>Crisia aculeata</i>				✓				
<i>Tubulipora plumosa</i>		✓	✓					
<i>Tubulipora liliacea</i>		✓	✓	✓	✓		✓	
<i>Tubulipora phalangea</i>		✓	✓	✓	✓		✓	
<i>Tubulipora lobifera</i>							✓	
<i>Diplosolen obelia</i>		✓	✓	✓	✓		✓	
<i>Plagioecia sarniensis</i>					✓		✓	
<i>Plagioecia patina</i>		✓	✓	✓	✓		✓	
<i>Patinella verrucaria</i>	✓	✓	✓	✓	✓	✓	✓	
<i>Disporella hispida</i>			✓	✓	✓	✓	✓	
Phylum: Bryozoa								
Class: Gymnolaemata								
Order: Cheilostomatida								
<i>Aetea anguina</i>								
<i>Aetea sica</i>	✓			✓	✓			
<i>Aetea truncata</i>	✓							
<i>Scruparia ambiagua</i>								
<i>Scruparia chelata</i>	✓							
<i>Conopeum reticulum</i>								✓
<i>Electra pilosa</i>	✓	✓		✓				✓

<i>Callopora lineata</i>	✓			✓	✓	✓	✓	✓
<i>Callopora dumerilii</i>		✓						
<i>Membraniporella nitida</i>							✓	
<i>Callopora craticula</i>		✓						✓
<i>Amphiblestrum flemingii</i>		✓			✓		✓	
<i>Bugula flabellata</i>				✓				
<i>Bugula turbinata</i>				✓				
<i>Cribrilina punctata</i>								✓
<i>Cribrilina annulata</i>					✓			
<i>Scrupocellaria reptans</i>	✓							
<i>Scrupocellaria scruposa</i>				✓	✓			
<i>Hippothoa flagellum</i>				✓	✓		✓	
<i>Celleporella hyalina</i>	✓						✓	✓
<i>Chorizopora brongniartii</i>				✓	✓			
<i>Escharoides coccinea</i>							✓	
<i>Escharella immersa</i>	✓	✓	✓	✓	✓		✓	✓
<i>Escharella ventricosa</i>				✓	✓			
<i>Escharella klugei</i>			✓	✓	✓			
<i>Escharella variolosa</i>	✓			✓				
<i>Porella concinna</i>				✓	✓			
<i>Reptadeonella violacea</i>				✓				
<i>Stomachetosella sinuosa</i>		✓		✓				
<i>Smittoidea reticulata</i>							✓	
<i>Parasmittina trispinosa</i>	✓	✓						
<i>Schizomavella auriculata</i>				✓				
<i>Schizomavella linearis</i>			✓	✓			✓	
<i>Microporella ciliata</i>	✓	✓	✓	✓	✓		✓	✓
<i>Fenestrulina malusii</i>	✓	✓		✓	✓		✓	
<i>Cellepora pumicosa</i>							✓	

2.4.3. Preliminary PRIMER analysis of epifaunal community data

Using epifaunal community data, a multidimensional scaling plot was used to graphically represent Bray-Curtis similarity between the sites (Figure 2.12). SIMPROF showed that most of the sites had very similar epifaunal communities with the exception of Loch Creran and Dornoch Firth. An examination of the SIMPER results showed that these differences were largely due to a different or reduced bryozoan fauna and a greater proportion of polychaetes or barnacles (Appendix C1 and C2). Loch Creran and Dornoch Firth were also the sites with the greater proportion of larger shells (Figure 2.14).

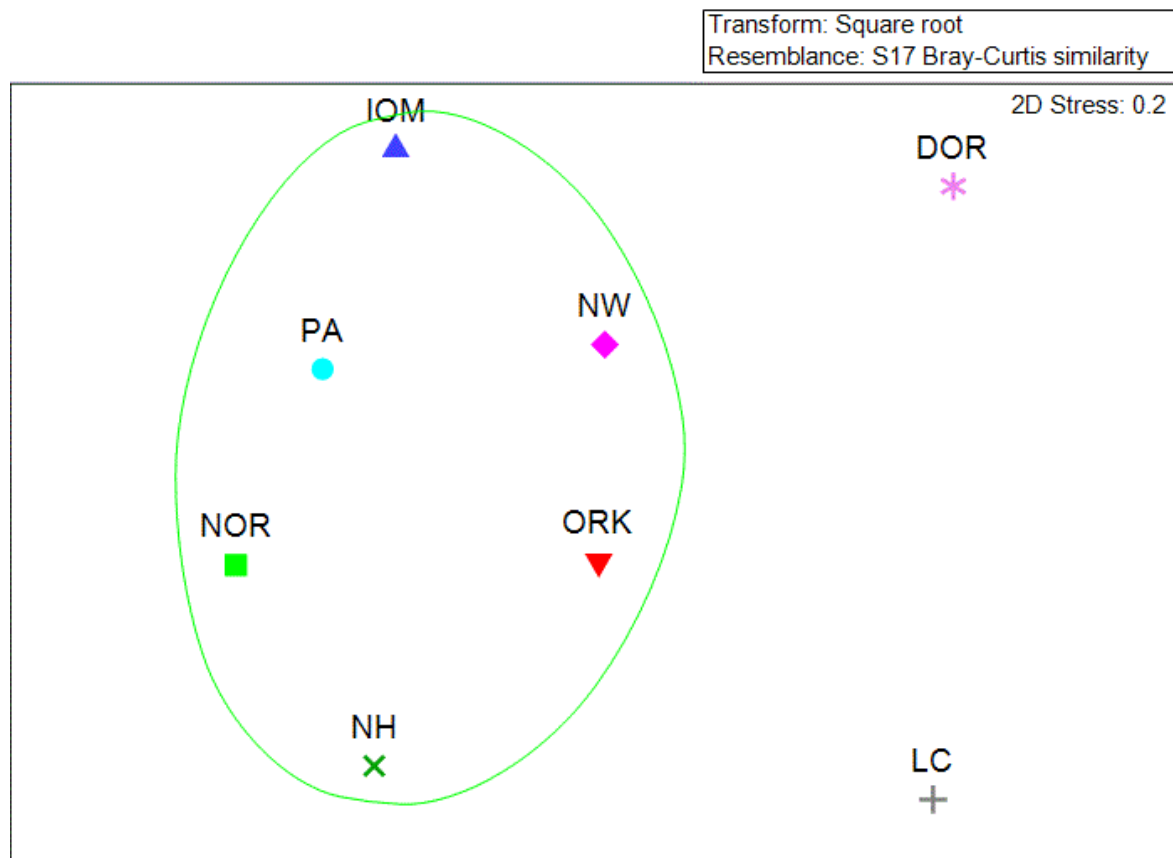


Figure 2.12: Multi-dimensional scaling plot of Bray-Curtis similarity between eight North-East Atlantic sites, green line indicate 3 groups (A, B, and C) supported by SIMPROF test, (group A: LC, group B: DOR; group C: IOM, ORK, NOR, NW, PA, and NH) ($n = 8$, 2D stress = 0.2). IOM: Ramsey Bay, Isle of Man; ORK: Karlsruhe wreck, Orkney; NOR: Skarnsundet West Bridge, Norway; NW: North Llyn; PA: Port Appin; LC: Loch Creran; NH: Noss Head; DOR: Dornoch Firth.

2.4.4. PRIMER analysis of epifaunal community shell quadrant regions

ANOSIM testing was conducted on combined both shell valves region data within each site such that the anterior and posterior regions and ventral and dorsal regions were compared. These tests highlighted that the epifaunal community on the anterior of the shell was significantly different to the posterior. Also the epifaunal community on the dorsal surface of the shell was often but not always significantly different to the ventral surface (Table 2.8, 2.9). Further analysis of combined anterior-posterior regions data are presented later in this section.

Table 2.8: Global ANOSIM results of similarity based on 9999 permutations on shell regions.

Site	Global R	Significance level %
Ramsey Bay	0.114	0.01
Karlsruhe wreck	0.125	0.1
Skarnsundet West Bridge	0.143	0.1
North Llŷn	0.189	0.1
Port Appin	0.187	0.1
Loch Creran	0.098	0.1
Noss Head	0.07	0.1
Dornoch Firth	0.152	0.1

Significant differences were found between all the epifaunal abundances of each shell region with the exception that region 2 did not differ from region 1 in Orkney, North Wales and Noss Head, and did not differ from region 4 in Loch Creran (Table 2.4).

Table 2.9: R values and significance of pairwise comparisons from analyses of similarities (ANOSIM) based on 9999 permutations of Ramsey Bay, Karlsruhe wreck, Skarnsundet West Bridge, North Llŷn, Port Appin, Loch Creran, Noss Head, Dornoch Firth horse mussel shell regions (significant differences in bold).

Ramsey Bay				Karlsruhe wreck		
R values	1	2	3	1	2	3
2	0.089			0.013		
3	0.206	0.143		0.303	0.237	
4	0.158	0.027	0.07	0.091	0.035	0.061
Significance%						
2	0.01			11.8*		
3	0.01	0.01		0.1	0.1	
4	0.01	2.7	0.06	0.1	1.3	0.2
Skarnsundet West Bridge				North Llŷn		
R values	1	2	3	1	2	3
2	0.047			-0.001		
3	0.262	0.275		0.339	0.375	
4	0.117	0.088	0.046	0.145	0.176	0.05
Significance%						
2	0.9			45.8*		
3	0.1	0.1		0.1	0.1	
4	0.1	0.1	1.2	0.1	0.1	0.4
Port Appin				Loch Creran		
R values	1	2	3	1	2	3
2	0.026			0.098		
3	0.309	0.344		0.262	0.046	
4	0.125	0.173	0.098	0.197	0.011	-0.002
Significance%						
2	3.5			0.1		
3	0.1	0.1		0.1	0.7	
4	0.1	0.1	0.1	0.1	13.4*	39.1
Noss Head				Dornoch Firth		
R values	1	2	3	1	2	3
2	-0.002			0.023		
3	0.132	0.145		0.266	0.264	
4	0.037	0.031	0.048	0.12	0.087	0.115
Significance%						
2	53.3*			2.4		
3	0.1	0.1		0.1	0.1	
4	1	2.2	0.1	0.1	0.1	0.1

* Not significant

SIMPER analyses were used to check for differences in the epifaunal species contributions between each shell region. SIMPER analysis highlighted key differences in the type of epifaunal community of each site.

The average similarity of the epifaunal communities making up each site were (Isle of Man 39.7%, Orkney 13.3%, Norway 32.8%, North Wales 19.4%, Port Appin 34.5%, Loch Creran 37.2%, Noss Head 29.1%, and Dornoch 25.3%). Therefore, sites Isle of Man, Loch Creran, Port Appin, and Norway horse mussels has a more similar epifaunal community composition

than Orkney, North Wales, Noss Head, and Dornoch sites, which can be largely attributed to higher abundances of the most common epifaunal species primarily *Spirobranchus triqueter* (Table 2.10, Appendix D1-D16) .

SIMPER was also used to investigate which taxonomic groups are more dominant at each site. The most common species were generally present within all shell regions and in a higher abundance in shell region 1 and 2 compared with regions 3 and 4, except in Noss Head site. In this locality *Spirorbis tridentatus* were higher in region 4 (Figure 2.13, Table 2.10).

Table 2.10: Epifaunal contributions across all sites based on Bray-Curtis similarity indices. Species contributing 60% or more are shown (highest contribution in bold).

Site	Average similarity%	Region	Dominant species	Contribution%
Ramsey Bay	39.7	1	<i>Spirobranchus triqueter</i> <i>Microporella ciliata</i> <i>Electra pilosa</i>	65.9
		2	<i>Spirobranchus triqueter</i> <i>Microporella ciliata</i> <i>Electra pilosa</i>	76.4
		3	<i>Spirobranchus triqueter</i> <i>Microporella ciliata</i> <i>Electra pilosa</i>	76.9
		4	<i>Spirobranchus triqueter</i> <i>Microporella ciliata</i> <i>Electra pilosa</i>	82.5
Karlsruhe wreck	13.3	1	<i>Spirobranchus triqueter</i> <i>Balanus balanus</i> <i>Patinella verrucaria</i>	80.4
		2	<i>Spirobranchus triqueter</i> <i>Balanus balanus</i> <i>Patinella verrucaria</i>	92.1
		3	<i>Spirobranchus triqueter</i> <i>Microporella ciliata</i> <i>Spirorbis tridentatus</i> <i>Patinella verrucaria</i>	74.0
		4	<i>Spirobranchus triqueter</i> <i>Balanus balanus</i> <i>Patinella verrucaria</i>	90.7
Skarnsundet West Bridge	32.8	1	<i>Spirobranchus triqueter</i> <i>Spirorbis tridentatus</i> <i>Tubulipora phalangea</i>	78.4
		2	<i>Spirobranchus triqueter</i> <i>Spirorbis tridentatus</i> <i>Tubulipora phalangea</i>	89.4
		3	<i>Spirobranchus triqueter</i> <i>Spirorbis tridentatus</i> <i>Tubulipora phalangea</i>	93.5
		4	<i>Spirobranchus triqueter</i> <i>Spirorbis tridentatus</i> <i>Serpula sp.</i>	93.6
North Llŷn	19.4	1	<i>Balanus balanus</i>	63.9

			<i>Escharella immersa</i> <i>Spirobranchus triqueter</i>	
		2	<i>Balanus balanus</i> <i>Escharella immersa</i> <i>Spirobranchus triqueter</i>	62.5
		3	<i>Reptadeonella violacea</i> <i>Spirobranchus triqueter</i>	70.5
		4	<i>Escharella immersa</i> <i>Spirobranchus triqueter</i> <i>Reptadeonella violacea</i>	73.6
Port Appin	34.5	1	<i>Spirobranchus triqueter</i> <i>Scrupocellaria scruposa</i> <i>Balanus balanus</i>	65.6
		2	<i>Spirobranchus triqueter</i> <i>Scrupocellaria scruposa</i> <i>Balanus balanus</i>	71.3
		3	<i>Spirobranchus triqueter</i> <i>Spirorbis tridentatus</i>	66.2
		4	<i>Spirobranchus triqueter</i> <i>Spirorbis tridentatus</i>	64.9
Loch Creran	37.2	1	<i>Spirobranchus triqueter</i>	99.3
		2	<i>Spirobranchus triqueter</i>	99.9
		3	<i>Spirobranchus triqueter</i>	98.7
		4	<i>Spirobranchus triqueter</i>	100
Noss Head	29.1	1	<i>Diplosolen obelia</i> <i>Membraniporella nitida</i> <i>Spirorbis tridentatus</i> <i>Escharoides coccinea</i>	58.5
		2	<i>Diplosolen obelia</i> <i>Membraniporella nitida</i> <i>Spirorbis tridentatus</i> <i>Spirobranchus triqueter</i>	62.5
		3	<i>Spirorbis tridentatus</i> <i>Escharoides coccinea</i> <i>Escharella immersa</i>	60.6
		4	<i>Spirorbis tridentatus</i> <i>Escharella immersa</i> <i>Spirobranchus triqueter</i> <i>Escharoides coccinea</i>	68.1
Dornoch Firth	25.3	1	<i>Balanus balanus</i> <i>Conopeum reticulum</i> <i>Balanus crenatus</i>	86.2
		2	<i>Balanus balanus</i> <i>Conopeum reticulum</i> <i>Balanus crenatus</i>	91.5
		3	<i>Balanus balanus</i> <i>Conopeum reticulum</i>	85.3
		4	<i>Balanus balanus</i> <i>Conopeum reticulum</i> <i>Balanus crenatus</i>	77.9

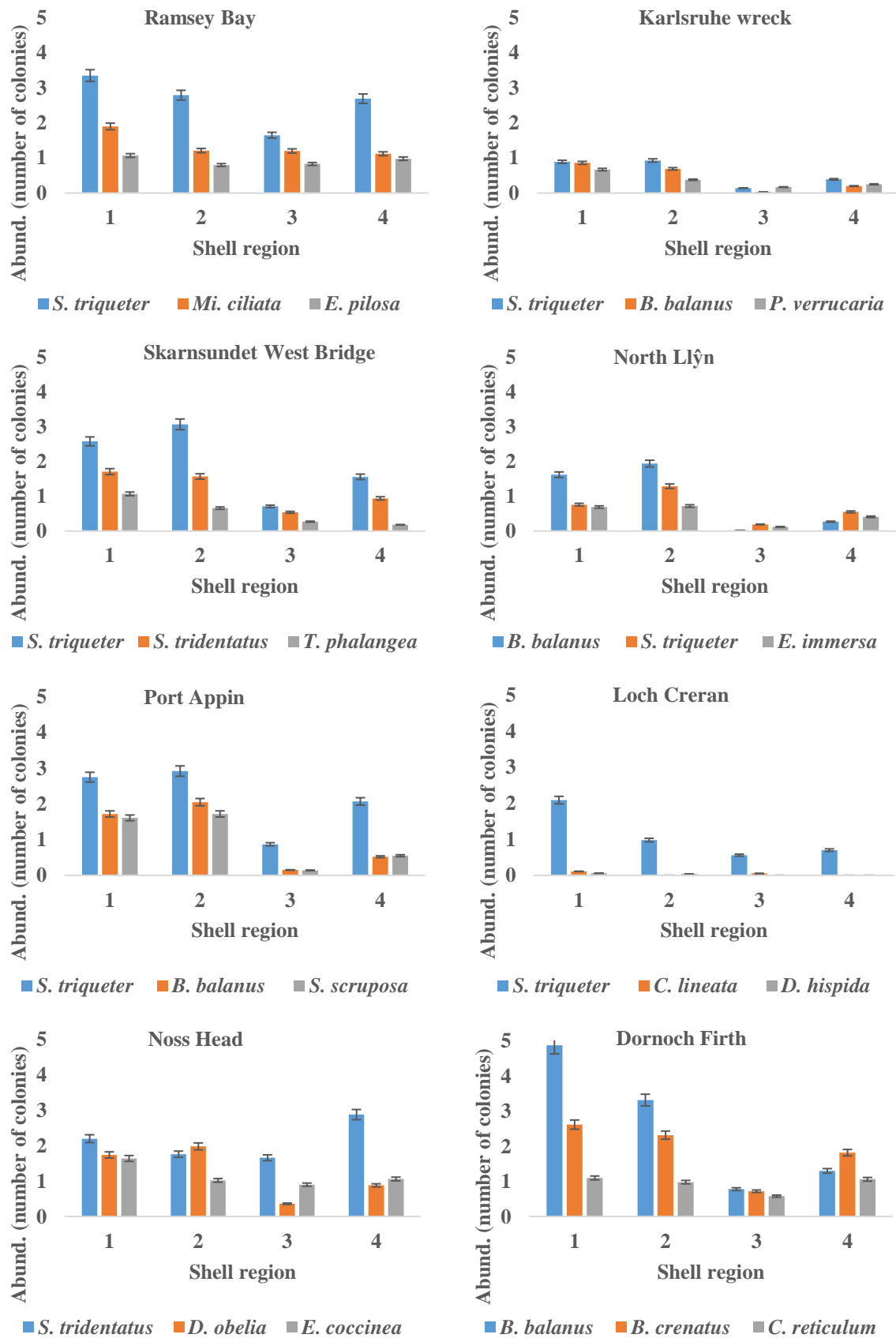


Figure 2.13: Abundances of dominant epifaunal species incrusting horse mussels within each shell region according to SIMPER analysis (error bars= standard deviation).

2.4.5. Diversity indices of shell epifauna

North Llŷn site had the highest number of species; Ramsey Bay had the highest number of colonies and Noss Head site had a higher level of diversity, based on Shannon Wiener diversity $H [Loge]$ (Table 2.11). Loch Creran and Dornoch Firth sites had the lowest numbers in total species. Loch Creran site had the lowest numbers in all diversity indices and the epifaunal community is less numerically equal than the other sites according to Pielou's evenness.

Table 2.11: Means of S, N, d, J, $H [Loge]$ and 1-Lamda from Ramsey Bay, Karlsruhe wreck, Skarnsundet West Bridge, North Llŷn, Port Appin, Loch Creran, Noss Head, Dornoch Firth sites.

Site	Total species (S)	Total individuals (N)	Species richness (d)	Pielou's evenness (J)	Shannon Wiener diversity ($H[Loge]$)	Simpson's diversity (1-Lamda)
Ramsey Bay	30	43.4	7.9	0.6	2.1	0.7
Karlsruhe wreck	23	8.5	10.2	0.7	2.3	0.9
Skarnsundet West Bridge	21	25.9	6.1	0.6	1.8	0.7
North Llŷn	37	17.3	12.6	0.6	2.4	0.8
Port Appin	34	39.8	8.9	0.6	2.2	0.8
Loch Creran	7	4.6	3.8	0.1	0.3	0.1
Noss Head	29	23.9	8.8	0.7	2.6	0.9
Dornoch Firth	12	14.7	4.1	0.7	1.8	0.8

2.4.6. Shell anterior and posterior regions

ANOSIM analyses showed that there is a significant difference between the anterior and posterior region in epifaunal abundance (Global R= 0.077 and significance level: 0.1%).

SIMPER analysis highlighted key differences in the type of epifaunal community of both anterior and posterior regions across sites (Table 2.12). The average similarities of the communities making up anterior and posterior regions were 15.07% and 26.47% respectively. Therefore, the posterior regions of the horse mussels have a more similar epifaunal community composition than the anterior region. The average dissimilarity in epifaunal communities between anterior and posterior regions was 81.69%, which can be largely attributed to higher abundances of the most common epifaunal species in the posterior region. Higher abundances of *P. triqueter*, *B. balanus*, and *S. tridentatus* together, contributed nearly 35% to the average dissimilarity shown between the anterior and posterior regions (Table 2.12).

Table 2.12: The epifaunal community composition between shell regions posterior and anterior provided by SIMPER analysis (average dissimilarity = 81.69).

Species	Posterior region Av.Abund	Anterior region Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.55	1.42	17.63	17.63
<i>Balanus balanus</i>	1.33	0.27	10.05	27.68
<i>Spirorbis tridentatus</i>	0.94	0.70	7.07	34.75
<i>Escharella immersa</i>	0.68	0.44	5.41	40.17
<i>Patinella verrucaria</i>	0.67	0.32	5.14	45.31
<i>Microporella ciliata</i>	0.61	0.43	4.62	49.92
<i>Diplosolen obelia</i>	0.47	0.20	3.49	53.42
<i>Tubulipora phalangea</i>	0.42	0.21	3.24	56.65
<i>Electra pilosa</i>	0.33	0.24	3.02	59.67
<i>Balanus crenatus</i>	0.23	0.12	2.63	62.31
<i>Tubulipora liliacea</i>	0.28	0.11	2.52	64.83
<i>Celleporella hyalina</i>	0.31	0.15	2.51	67.34
<i>Conopeum reticulum</i>	0.14	0.12	2.25	69.59
<i>Scrupocellaria scruposa</i>	0.37	0.09	2.16	71.75

2.4.7. Analysis of anterior-posterior diversity indices

The posterior region of the shell had a slightly higher diversity, based on Shannon Wiener diversity $H' [\text{Loge}]$ index (Table 2.13). The total epifaunal species and number of individuals were also higher in the posterior regions of the horse mussel shells. Although diversity appears to be greater in the posterior region, the community was consistently even between anterior and posterior shell regions according to Pielou's evenness.

Table 2.13: North-East Atlantic horse mussel shell diversity indices between anterior and posterior shell regions (n=400).

Region	Total Species (S)	Total individuals (N)	Species richness (d)	Pielou's evenness (J)	Shannon Wiener diversity ($H' [\text{Loge}]$)	Simpson's diversity ($1-\text{Lambda}$)
Posterior	54	31.3	15.3	0.6	2.7	0.9
Anterior	49	13.4	18.5	0.6	2.6	0.9

2.4.8. Size frequency of horse mussel shells

Horse mussel shells from eight sites across the North-East Atlantic vary in size. The Karlsruhe wreck and Skarnsundet West Bridge sites had a wide range of size classes. The Noss Head site had the greatest proportion of smaller shells but Loch Creran and Dornoch Firth had a greater proportion of larger shells (Figure 2.14).

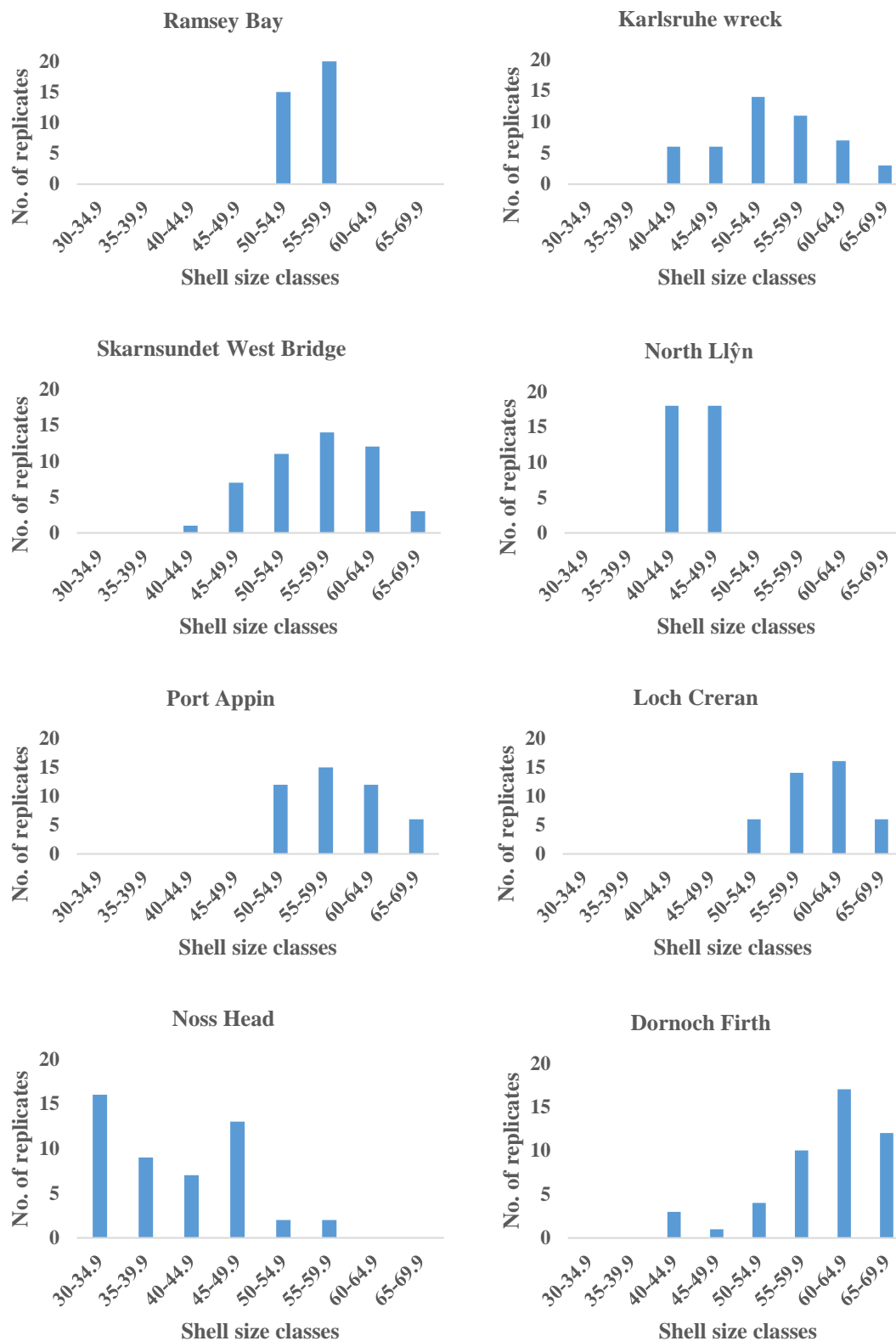


Figure 2.14: Horse mussel size classes based on the lengths of 400 horse mussels (mm).

2.4.9. PRIMER analysis of epifaunal community diversity relationship to shell size classes

ANOSIM analyses on horse mussel shell size class data showed that there was a significant difference between the epifaunal abundance of shell size classes (Global R= 0.122 and significance level: 0.1%). The epifaunal abundance on the five smaller size classes (30-34.9, 35-39.9, 40-44.9, 45-49.9, 50-54.9) was always significantly different from the two larger size classes (60-64.9, 65-69.9) as shown in Table 2.14.

Table 2.14: R values and significance of pairwise comparisons from analyses of similarities (ANOSIM) based on 9999 permutations of North-East Atlantic horse mussel's shell size classes (significant differences in bold).

R values	30-34.9	35-39.9	40-44.9	45-49.9	50-54.9	55-59.9	60-64.9
35-39.9	-0.114						
40-44.9	0.046	-0.058					
45-49.9	0.024	0.091	0.08				
50-54.9	0.218	0.159	0.205	0.129			
55-59.9	0.188	0.153	0.211	0.116	-0.013		
60-64.9	0.383	0.355	0.254	0.222	0.048	0.012	
65-69.9	0.507	0.406	0.144	0.328	0.153	0.096	0.053
Significance%							
35-39.9	94*						
40-44.9	22.4*	70.1*					
45-49.9	33.6*	84.2*	0.5				
50-54.9	0.6	7.1*	0.1	0.1			
55-59.9	0.6	5.9*	0.1	0.3	80.7*		
60-64.9	0.1	0.1	0.1	0.1	0.4	18.2*	
65-69.9	0.1	0.1	0.2	0.1	0.3	3.4	4

* Not significant

SIMPER analyses were used to check for differences in the epifaunal community abundances on horse mussels between each shell size class. SIMPER analyses showed that polychaetes numbers were highest at the shell size class (50-54.9) then decreased slightly with the increase of shell size. Bryozoan abundance was higher in lower shell size classes (30-34.9, 35-39.9) that decreased with the increase of shell size, and barnacle numbers were highest at the largest shell size class (65-69.9) as shown in Figure 2.15.

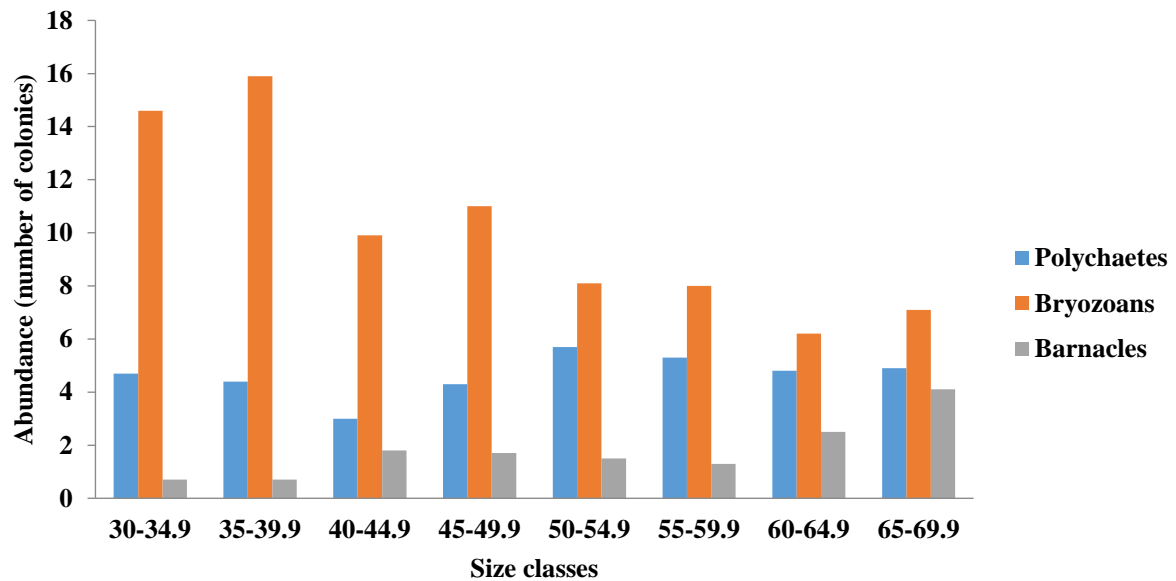


Figure 2.15: Abundances of epifaunal species groups incrusting on horse mussels within each shell size class according to SIMPER analysis.

2.4.10. Diversity analysis of shell size classes

Shell size classes 50-54.9, and 55-59.9 had the highest number of species; the small size class 35-39.9 had the highest number of species colonies and 40-44.9 size class had a higher level of diversity, based on Shannon Wiener diversity $H' [\text{Loge}]$ (Table 2.15).

Table 2.15: Means of S, N, d, J, $H' [\text{Loge}]$ and 1-Lamda for shell size classes in Ramsey Bay, Karlsruhe wreck, Skarnsundet West Bridge, North Llŷn, Port Appin, Loch Creran, Noss Head, Dornoch Firth sites.

Shell size classes	Total species (S)	Total individuals (N)	Species richness (d)	Pielou's evenness (J)	Shannon Wiener diversity ($H' [\text{Loge}]$)	Simpson's diversity (1-Lamda)
30-34.9	26	20.4	8.2	0.8	2.9	0.9
35-39.9	25	21.5	7.8	0.9	2.9	0.9
40-44.9	40	13.5	14.9	0.8	3.2	1.0
45-49.9	38	17.4	12.4	0.8	3.1	0.9
50-54.9	43	15.4	15.3	0.7	2.9	0.9
55-59.9	43	15.1	15.4	0.7	3.0	0.9
60-64.9	38	13.5	14.1	0.7	2.8	0.9
65-69.9	30	16.3	10.3	0.8	2.8	0.9

2.5.Discussion

The overall aim of this study was to investigate the factors influencing biodiversity, abundance, spatial distribution and successional patterns of encrusting epifaunal communities.

2.5.1. Biodiversity

The epifaunal community of horse mussels was analysed from 400 individuals from Skarnsundet West Bridge, Norway in the North to Llŷn Peninsula in the South. The null hypothesis that the epifaunal community would not vary with position on the shell and shell size was rejected. At least 54 epifaunal species (Table 2.7) were seen to colonise the shells of horse mussels from eight sites across the North-East Atlantic showing that horse mussels are able to support high levels of epifaunal biodiversity. The epifaunal communities were similar in some sites, except in Loch Creran and Dornoch Firth the epifaunal communities were quite different as revealed by the MDS plot (Figure 2.12). All sites shell epifauna were dominated by encrusting, calcareous species, such as the polychaete worm *Spirobranchus triqueter*, the barnacle *Balanus balanus*, and the ubiquitous bryozoan *Escharella immersa*. Loch Creran and Dornoch Firth, however, had much reduced bryozoan communities in keeping with the larger shell sizes at these sites (Section 2.4.8, Appendix D11, 15).

2.5.2. Shell regions

Preliminary results showed that the high level of significant differences between the communities in each of the quadrants on the shells was not reflecting an ecologically meaningful situation but rather that there were low species abundances in each sample. To mitigate this, the data for combined shell regions 1 and 2 as well as combined regions 3 and 4 was used so that comparisons could be made between anterior and posterior regions of the shells based on greater abundances to give improved statistical power. As a result, and unlike the quadrant data, the anterior-posterior combined data showed significant differences across all the sites. Statistical analyses did not support the hypothesis that different regions of the shell support hugely different epifaunal communities, as the R significance was relatively low in multivariate testing.

The epifaunal community of the anterior shell was shown to be significantly different to the posterior. The posterior surface of horse mussel shells was more diverse in epifaunal species. That might be due to *M. modiolus* can be found partially buried in soft sediments (Pearce and LaBarbera, 2009). The extent at which horse mussels are buried in sediments varies greatly and is a common behavioural feature; therefore, it is likely that shell regions which are

significantly less epifaunally abundant were at least partially buried at some point in the horse mussel life history. Burying in sediments brings about stability in horse mussel beds, but mussels are also angled in such a way that they receive the maximum input of particulate food without compromising their stability. The region of the shell that is buried and the angle at which it is buried will affect the local hydrographical regime. The anterior region of the shells was lower in epifaunal species and colonies numbers as well as slightly lower in diversity, that maybe due to the abrasion effect close to the sediment caused by the movement of sand, gravel, and algal fragments will also affect the communities composition. Shell abrasion on the seabed is considered to be a continuous process where particles and sediments are released into the water column and eventually enter the food chain (Thompson and Amos, 2002).

Behavioural responses in horse mussels, such as, intensive clumping was observed at the Noss Head site which had the highest level of diversity than other sites, which can be explained that Noss Head had the most developed clump structure and the mussels were extremely dense and formed clumps that were raised from the seabed such that many of the mussels in the clumps were not in contact with the seabed. This clumping behaviour provides two advantages for the mussels and their encrusting epifaunal communities. First it is a protective mechanism against crabs, lobsters and drilling gastropods. Differences in orientation of individual mussels within the clump make it hard for those predators to reach mussels in the centre of a clump only allowing them to prey around the outside edge. A second advantage is that intensive clumping protects mussels from dislodgement by physical disturbances (Casey and Chattopadhyay, 2008).

As the posterior shell region was the most diverse, it is possible that the filter feeding currents generated by horse mussels provide their epifauna with an enhanced food source. Both the inhalant and exhalant siphons are found within the posterior region of the shell (Dinesen and Morton, 2014) as shown in Figure 2.1, therefore small-scale current flow generated by the horse mussel filter feeding may affect larval settlement and provide higher amounts of food. Larvae of invertebrate animals such as barnacles, polychaetes, bryozoans, hydroids, and sponges tend to settle on rough surfaces exposed to moving water, some settling in grooves or pits, around the bases of bumps in bivalves. Field measurements by Koehl et al. (2013) revealed that individuals within clusters such as mussels were protected from strong hydrodynamic forces. Also the spacing between tube worms, barnacles and bryozoans affects

the water flow between them, as well as where surrounding water currents deposit food particles or sweep them off the substratum.

Exposure to a greater flow velocity may also be responsible for the higher levels of epifaunal diversity associated with the posterior region of the shell. Many benthic sessile invertebrates produce planktonic larvae which are transported by currents and colonize new surfaces. The recruitment of larvae to benthic sites is a critical process affecting community structure. To colonize a surface, a larva must be transported to that surface, settle (i.e. attach to the surface), and recruit (i.e. metamorphose into a juvenile and survive) (Koehl et al., 2013). The quality of the site at which larvae make the permanent transition from the water column to the substrate has deep implications for individual fitness and ultimately determines distribution and abundance within populations (Burgess et al., 2009). The settlement of invertebrate larvae is influenced by specific physical, chemical and biological factors from a variety of sources in the environment. Such factors may be related to the physical surfaces of substrata; the microbial bio-films associated with the substrata; the presence of con-specific adults, or specific prey (Yu, 2007). Individuals that settle near dominant competitors are more likely to die quickly, as are those that settle within the range of predators or where disturbance events frequently occur. Organisms located in spaces of refuge, increase their chances of survival against competitors, predators, and disturbance events. Size can also be protective to colonies once they have grown to certain dimensions unaffected by competitors; this is the size refuge (Yu, 2007).

The North Llŷn site had the highest number of species while Ramsey Bay had the highest number of colonies and Noss Head site had a higher level of diversity, based on Shannon Wiener diversity $H' [\text{Loge}]$ (Table 2.11). All three sites are characterized by presence of fast tides (Hydrographic office, 1992, 2017a, 2017b). These findings are supported by the following study by Reidenbach et al. (2009), who reported the exposure to fast current flow means exposure to higher levels of passing larvae allowing epifaunal colonisation as well as the supply of dissolved gases, nutrients and from which their wastes, gametes, larvae, or spores can be dispersed.

2.5.3. Shell size

Results showed significant correlations between shell size, and species abundance. Bryozoan abundance was higher in lower shell size classes that decreased with the increase of shell size which might be due to small shells increasing the probability of bryozoan species dominance,

because the colonies are able to occupy a major proportion of the available space on the small shells. A study by Osman (1977) reported that bryozoan species can develop long term dominance on small substrata but on larger ones bryozoan dominance happens apparently at a slower rate that will result in low species numbers and diversity because of extremely uneven distribution. As substrate size increases, the increased time of species stability might be expected to increase the probability of dominance on the substratum that should cause a decrease in the average diversity with increased size (Osman, 1977). In the present study, polychaetes and barnacle numbers were also highest in the medium and large shell size class. There are similarities between these results and a study by Tsuchiya (2002) who investigated the effect of *Mytilus edulis* mussels size on the composition of encrusting species and reported the dominance of polychaete and barnacle species occurred on medium and large mussels, and that they were not common on smaller ones which might be due to the competition between polychaetes and bryozoans for food and space. Like bryozoans, polychaetes are filter feeders and their larvae are able to locate shell regions suitable for settlement and significantly settle around the respiratory siphons on posterior region of the shell (Gray and Kaiser, 2007). With the increase of shell size polychaete populations may increase in density on shells as surface fouling and may prevent space availability for bryozoan species.

2.5.4. Summary and conclusions

Overall, specific factors were found to be important to both the development and distribution of the epifaunal communalities on the horse mussel shells such as the preference of the posterior region as a site of attachment; the dominance of more than one species on the shell substratum; and the size of shells. Horse mussels modify the community structure of epifaunal benthic organisms by their selective particle feeding, therefore, if physical sediment disturbance by tidal currents, increased wave action/storm events and fisheries activities occurred it might influence the structure and ecosystem function of the epifaunal species communities (Kanaya et al., 2005). Scallop dredging and trawling fishing gears have a detrimental effect on the viability of many non target benthic species by removing and killing many infaunal and epifaunal species that will reduce the structural complexity of the seabed, and alter the diversity and composition of benthic assemblages (Boulcott et al., 2014). Suspended sediment and increased turbidity can cause lethal effects in benthic organisms resulting in changes to water quality and quantity of food supply that could inhibit feeding. Also partial or complete burial caused by disturbance could smother epifaunal species

underneath the sediments and prevent gas exchange causing suffocation (Hinchey et al., 2006).

In a recent study by Kuklinski et al. (2014), the factors controlling the first development of polar bryozoan assemblages were investigated. They reported that both species richness and abundance of local adult populations are important factors in controlling recruitment and there was a correlation between the number of bryozoan adult colonies and number of recruits. Since the majority of Antarctic bryozoans have limited dispersal larvae, Kuklinski et al. (2014) found no single bryozoan larva in the plankton from above the sea bottom in sampled locations which matched the diversity patterns observed between newly recruited assemblages and nearby adult assemblages.

Because of the nature of horse mussel beds, the species of marine epifaunal communities living on the shells occur in distinct patterns of distribution. This system is ideal for studying the magnitude and variability of the disturbances on species distribution and community composition as well as their ecological effects. Clear understanding of the dynamics and ecosystem services of these habitats as filter feeding units for improving of water quality and nutrient cycling, can help to develop policies for managing human exploitation of coastal assemblages and for increasing knowledge regarding the resilience and for promoting restoration of habitats which have suffered damage (Airolidi et al., 2005).

3. Chapter 3: Bryozoan competitive interactions in the North-East Atlantic

3.1. Introduction

Diverse marine communities of animals and plants are associated with abiotic substrates such as coarse sand grains, pebbles, cobbles and boulders, rocky platforms, and biotic hard substrates that include shells and skeletons of both living and dead organisms of mobile and sessile species. Sessile invertebrates recruit onto hard substrates via a dispersive larval phase and most are suspension feeders consuming phytoplankton (Taylor, 2016).

3.1.1. Life cycle of sessile invertebrates

Most sessile marine benthic invertebrates have two stages of their life cycles; an adult sessile stage alternating with a mobile and dispersive larval phase. The larval stage duration has an effect on the adult distribution. The longer the larvae continue at the planktonic stage, the further they can be distributed. Settlement refers to a process of transformation from a pelagic to a benthic stage of life that ends with metamorphosis, while recruitment is a process of establishing a population including settlement and all early post settlement events (Ronowicz et al., 2014). This type of life cycle is typical for marine Bryozoa (Sharp et al., 2007) as illustrated in Figure 3.1.

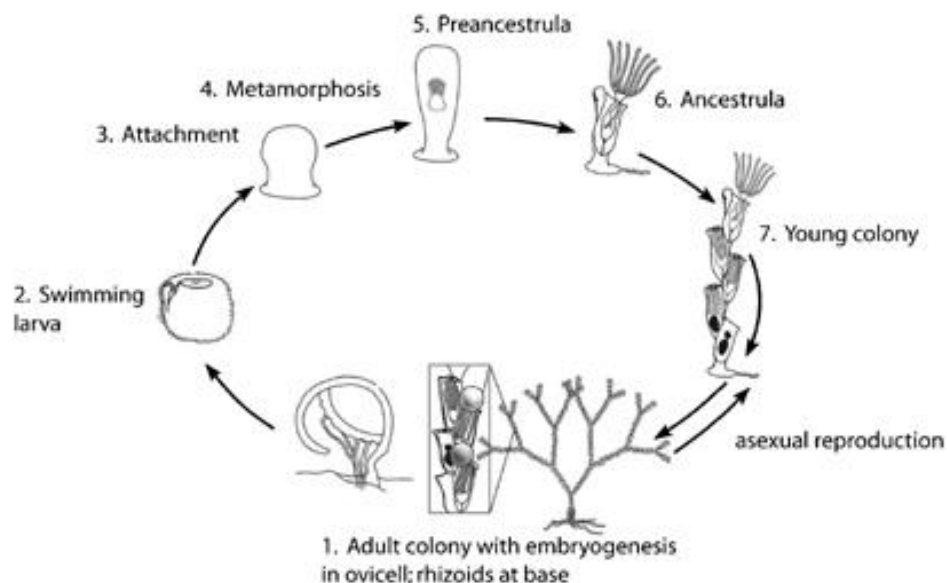


Figure 3.1: Life cycle of the Chlestone bryozoan *Bugula*. 1: adult *Bugula* with embryos in ovicells, 2: swimming larvae released from ovicells remain in water column for a variable period of time. 3-6: larval settlement, metamorphosis and development into the ancestrula. 7: budding of new zooids to form a mature colony Sharp et al., 2007).

3.1.2. Availability of resources

In the marine environment, organisms compete for their share of limited resources for access to food and space (Barnes and Kuklinski, 2005). Interactions among organisms have implications for the survival and reproduction of individuals and ultimately, the survival and evolution of populations and species (Liow et al., 2016). Solitary and colonial animals on encrusting marine hard substrata have different abilities to use space. Colonial forms are generally superior competitors for space because their growth allows continuous lateral occupation of substrates without the need for sexual reproduction and recruitment, and they are less susceptible to being fouled. Solitary animals include polychaetes and barnacles; these survive in the marine environment because of various morphological and behavioural characteristics such as their size, and aggregative behaviour that protects them in a competitive interaction with colonial animals (Jackson, 1977). In addition, competition between colonial species results in partial mortality that means colonies can be partly overgrown and yet survive, whereas overgrowth of solitary species is more often fatal (Taylor, 2016).

3.1.3. Marine Bryozoa

Bryozoans are a large and diverse group of colonial, benthic marine invertebrates. They inhabit a wide range of environments with a variety of salinities and temperatures. The majority of bryozoan taxa belong in the order Cheilostomata class Gymnolaemata (Amini et al., 2004). Liow et al. (2016) hypothesized that Cyclostomata bryozoans are poor competitors compared to Cheilostomata due to the latter having a high species diversity.

3.1.4. Bryozoan colony morphology

Bryozoan colonies consist of multiple small modules called zooids, which feed using ciliated lophophores that induce water currents, from which food particles are ingested. The growing success of zooids varies with extrinsic factors such as external flow currents and food content in the surrounding waters, the presence of neighbouring colonies, as well as colony characteristics such as colony growth form and the specialization of zooid morphologies (Griinbaum, 1997). Bryozoan morphological changes can be induced by aggressive competitive interactions by other bryozoan species or colonial marine invertebrates (Padilla et al., 1996).

Bryozoan species attached to hard substrata, have a number of morphological types, including encrusting sheet and erect branching tree forms. The outcomes of competitive interactions can be strongly influenced by the morphologies of the competitors. Erect branching forms are relatively isolated from the substrata-associated competitors, whereas sheet forms encrust the substratum (Walters and Wethey, 1991). The zooids in encrusting sheets are generally densely packed in a two-dimensional layer, and stay in contact with the substrata which has some advantages; firstly the bryozoan colony can encrust a large amount of space and eliminate competitors and secondly the close proximity of feeding zooids in a sheet provides the opportunity for coordinated feeding currents or dispersal of sperm via an exhalant chimney arrangement (e.g. in *Membranipora membranacea*). However, encrusting sheets might be susceptible to overgrowth along their edges (Pratt, 2004). Thin sheets tend to lose to thicker forms unless they have a height advantage in the zone of contact. Therefore, one would predict that animals with thin, sheet-like growth forms should preferentially settle on or near locations where they have a height advantage (Walters and Wethey, 1991).

3.1.5. Competitive interactions

Space is a primary limiting resource for Bryozoa that subsequently leads to competition for space among the settled organisms (Nandakumar et al., 1993). Darwin believed that competition leads to natural selection and ultimately evolution not just within the same species, but also between different classes and phyla (Barnes, 2002). The outcomes of competition can be of four types. Overgrowth interaction occurs when one competitor wins and the other loses and in extreme cases result in death. Another possible interaction for a potential competitor is a draw or tie results in a standoff; this is known to be common in sessile and colonial animals (Barnes and Kuklinski, 2005). Fouling interaction results when a larva settles onto the living surface of an established colony. A reciprocal interaction occurs when one species overgrows another along part of their contact but the interaction is reversed elsewhere along the contact (Taylor, 2016). These interaction types are illustrated diagrammatically in Figure 3.2.

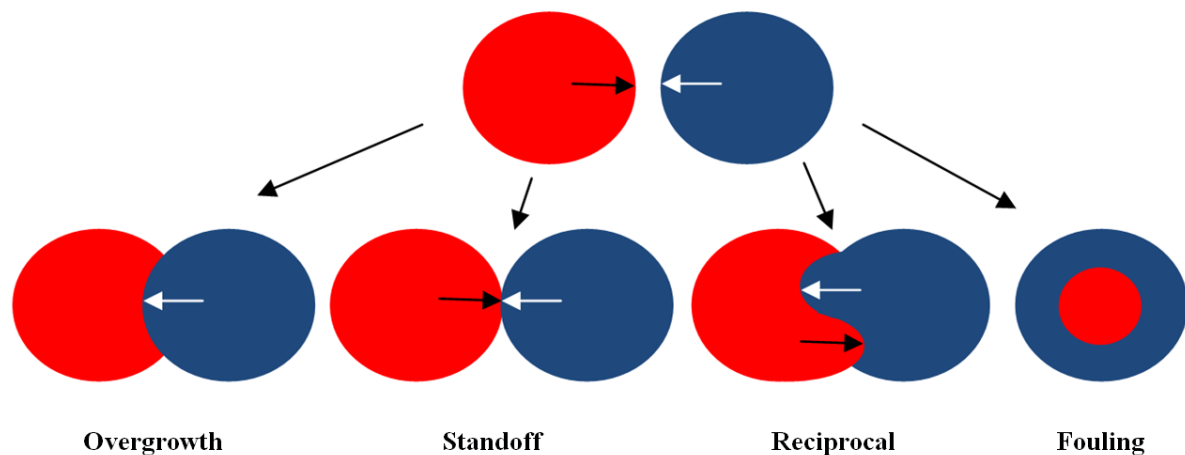


Figure 3.2: Diagram of the four possible competition outcomes (overgrowth, standoff, fouling and reciprocal) of marginal encounters between two colonies (colour-coded red and blue) competing for substrate space.

Modiolus modiolus beds can be regarded as habitat islands because they provide space for bryozoan colonization. The zooids in encrusting sheets stay in contact with the substratum and experience slower water velocities associated with the velocity gradient that exists close to the substratum. Therefore, the zooids are protected from the forces of fast flow (Pratt, 2004). Since bryozoans are preserved precisely in their life positions they provide excellent natural systems to study ecological interactions between bryozoan species and their host. Such studies may include larval settlement behaviour, substrate selection, standoff and overgrowth interactions. There is no published study to date which details the competitive interactions of epifauna on *Modiolus modiolus* horse mussels in biogenic reef habitats, in the northern Hemisphere. However competition between encrusting bryozoan has been studied on other substrata such as rocks (Barnes, and Rothery, 1996), and panels (Gappa, 1989; Padilla, 1996; Nandakumar and Tanakam, 1997). The recent study by Liow et al. (2016) investigated whether overgrowth interaction outcomes in fossil bryozoan species change on a macro-evolutionary timescale. The study reported the following: (1) some species are constant winners, and others are constant losers, while in other species, winning and losing seem to happen equally. (2) In genus-level interactions, some genera are clear winners such as *Escharoides*, and *Valdemunitella*, while other genera *Microporella*, *Fenestrulina* and *Parasmittina* varied in competitive abilities suggesting a strong inter-specific variation in competitive ability. (3) Few species changed their winning proportions through their evolution, suggesting stability in competitive abilities on the timescales of thousands of generations.

In this study, the ecological factors of the horse mussels *Modiolus modiolus* substrate such as colonization position and space availability in relation to size are investigated in order to establish if these factors influence competition between bryozoan species.

3.2. Aim and objectives

The overall aim of this study is to investigate competitive interactions of sessile epifaunal cover on the shells of horse mussel *Modiolus modiolus* from eight horse mussel beds throughout the geographical range of the species.

The objectives of the study are:

1. To identify the competitive bryozoans to species level in each competitive interaction type.
2. To record the number of bryozoan competitive interactions in each site and in the anterior- posterior shell regions of horse mussels.
3. To record the number of competitive intrection types in all sites .
4. To analyse the level of bryozoan competition in each of the competitive interaction types and in horse mussel shell size classes using PRIMER v7 software.
5. To identify and quantify competitive bryozoans to species level on panels from Karlsruhe wreck site.

3.3. Material and methods

3.3.1. Identification of competitive species

A Leica MZ7.5 high-performance stereomicroscope was used to identify species and record any competitive relationships between bryozoans on horse mussel shells and on panels deployed at the Karlsruhe wreck site. Scanning Electron Microscopy was used where required to confirm species identity.

3.3.2. Type of interaction

The numbers of competitive interactions between bryozoan species were measured on each shell as an indicator of competition. Competitive interactions were classed as ‘species overgrowth’ when one colony margin grows over the other. Other types of bryozoan interactions were ‘standoff’, where neither the colonies margins get the upper hand and overgrow the other, ‘reciprocal overgrowth’ when colony A grows over colony B at one point, while colony B grows over colony A at another point and ‘fouling’ when one colony had grown entirely on top of the other. This definition of terms is in line with previous studies including (Liow et al., 2016; Taylor, 2016) to allow direct comparisons with these prior studies.

3.3.3. Data collection for competitive interactions

The numbers of colonies of competing bryozoan species observed on horse mussel shell regions (posterior-anterior) were recorded to know which region on the horse mussel shell support the highest level of species interactions. Bryozoan species were listed in an Excel spreadsheet with their colony numbers in each interaction. In cases of overgrowth, the winning colonies were recorded as (W) and the losing colony as (L), standoff (S), fouling (F) and reciprocal (R) (Appendix G).

3.3.4. Data analysis of competitive interaction

Univariate diversity indices were used to test for differences in bryozoan competitive interaction between the posterior and anterior regions using IBM SPSS Statistics 20 software. Multivariate analyses were conducted using the software PRIMER v7. ANOSIM analyses of similarity (9999 permutations), were used to test for differences between the abundances of competitive interaction types (winning, losing, standoff, fouling, and reciprocal) between bryozoans species across the North-East Atlantic. ANOSIM analyses were also used to test for differences between the shell size classes in relation to competition. SIMPER was used to

describe which bryozoan species were responsible for the dissimilarity between the competitive interactions types and size classes. The following hypotheses were tested:

1. There is no significant difference between the incidence of competition interaction and location on the shell.
2. There is no significant difference between the incidences of competition interaction types.
3. There is no significant difference between the incidences of competition interaction with a change in horse mussel shell size.

Diversity indices were calculated using each of the competitive interactions data to give an understanding of the level of epifauna in the different types of interactions. Total species (S), total individuals (N), Species richness (d), Pielou's evenness (J), Shannon Wiener diversity ($H' = -\sum p_i \log p_i$) and Simpson's diversity ($1/\sum p_i^2$) were calculated.

3.4.Results

3.4.1. Light microscope images for species identification

Competitive species identifications were largely conducted using light microscopy. Selections of the competitive species identified are illustrated in Figures 3.3-3.8.

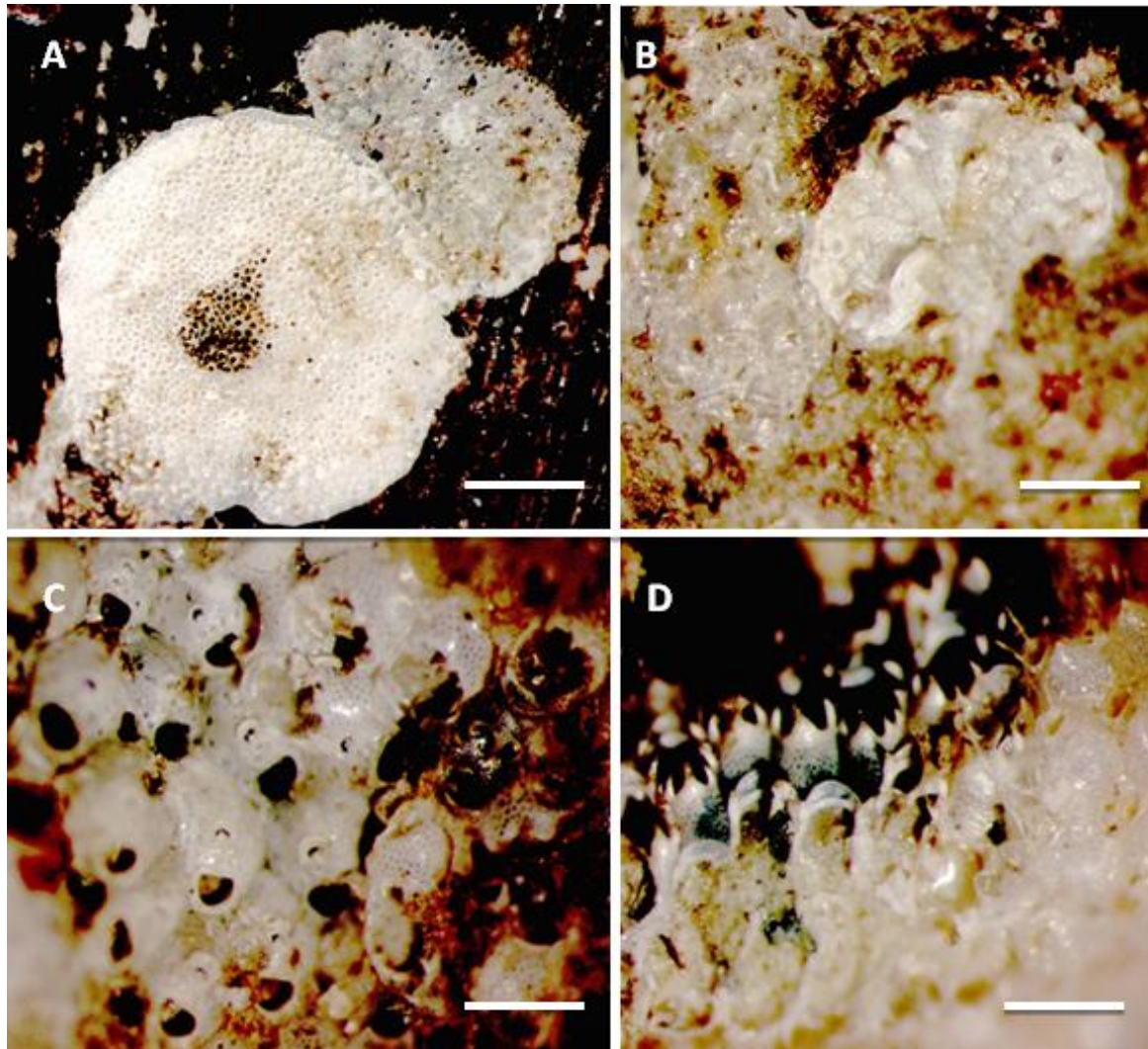


Figure 3.3: Ramsey Bay, Isle of Man bryozoan species competitive interactions on horse mussel shells. A: standoff interaction between upper colony *Plagioecia patina* and lower colony *Patinella verrucaria*, (scale bar= 2.5 cm). B: standoff interaction between right colony *Tubulipora phalangea* and left colony *Chorizopora brongniartii*, (scale bar= 2.5 cm). C: overgrowth interaction between right colony *Electra pilosa* (winning) and left colony *Fenestrulina malusii* (losing), (scale bar= 1.5 cm). D: overgrowth interaction between upper colony *Electra pilosa* (losing) and lower colony *Microporella ciliata* (winning), (scale bar= 2 cm).

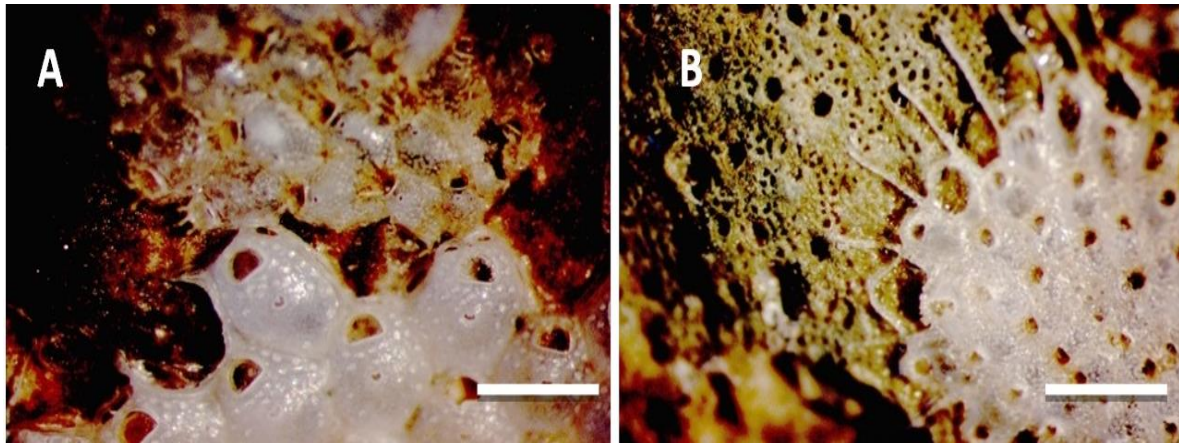


Figure 3.4: Karlsruhe wreck, Orkney bryozoan species competitive interactions on horse mussel shells. A: standoff interaction between upper colony *Microporella ciliata* and lower colony *Fenestrulina malusii*, (scale bar= 1 cm). B: *Escharella immersa* is fouling on top of *Parasmittina trispinosa* colony, (scale bar= 2 cm).

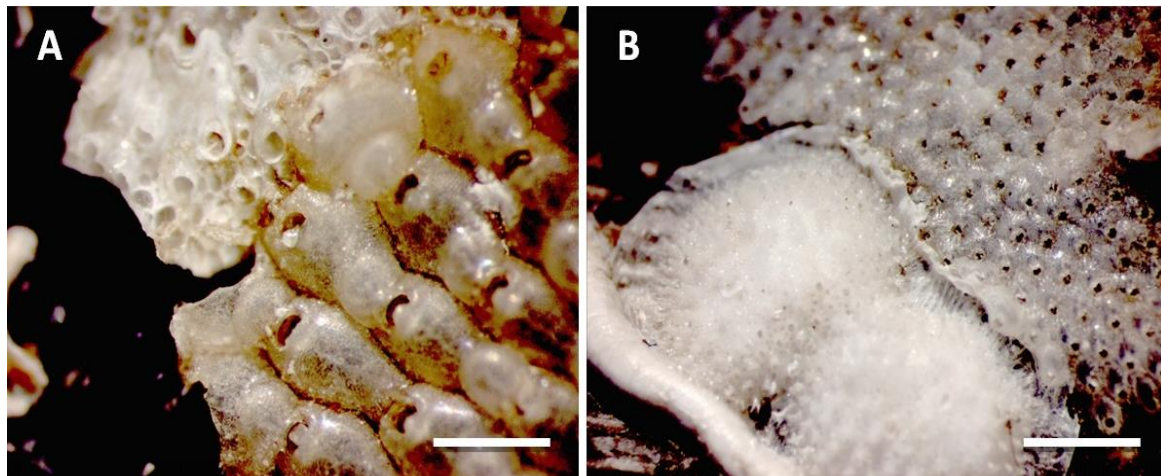


Figure 3.5: Skarnsundet West Bridge, Norway bryozoan species competitive interactions on horse mussel shells. A: overgrowth interaction between upper colony *Diplosolen obelia* (losing) and lower colony *Escharella klugei* (winning), (scale bar= 1 cm). B: overgrowth interaction between upper colony *Escharella immersa* (winning) and two lower colonies *Patinella verrucaria* (losing), overgrowth interaction between *Patinella verrucaria* colonies upper colony (losing) lower colony (winning) (scale bar= 2.5 cm).

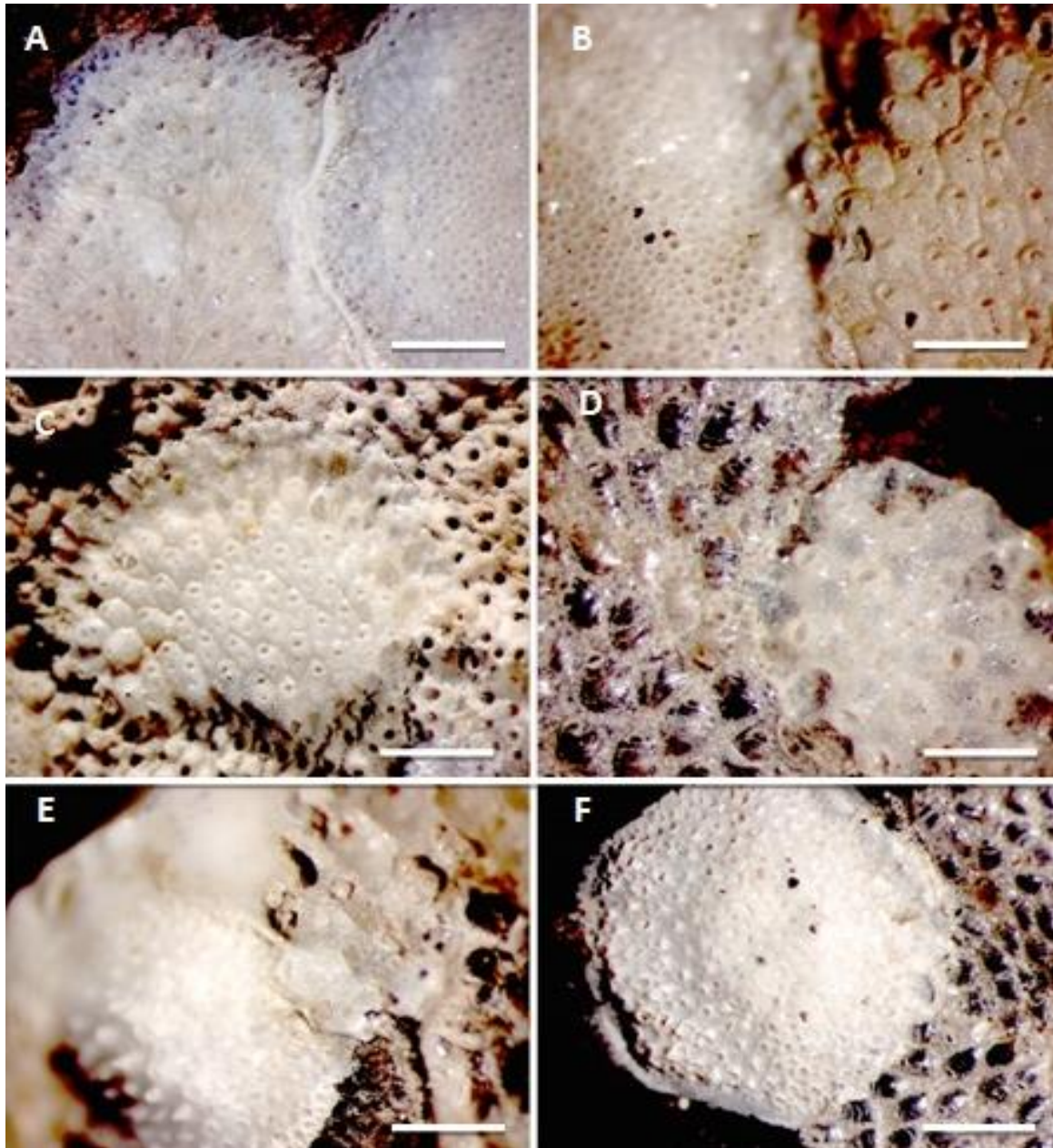


Figure 3.6: North Llŷn bryozoan species competitive interactions on horse mussel shells. A: overgrowth interaction between right colony *Patinella verrucaria* (winning) and left colony *Diplosolen obelia* (losing), (scale bar= 2 cm). B: overgrowth interaction between right colony *Reptadeonella violacea* (winning) and left colony *Patinella verrucaria* (losing), (scale bar= 1.5 cm). C: *Reptadeonella violacea* is fouling on top of *Stomachetosella sinuosa* colony, (scale bar= 1.5 cm). D: overgrowth interaction between right colony *Reptadeonella violacea* (winning) and left colony *Chorisopora brongniartii* (losing), (scale bar= 1 cm). E: overgrowth interaction between right colony *Fenestrulina malusii* (winning) and left colony *Patinella verrucaria* (losing), (scale bar= 1 cm). F: standoff interaction between right colony *Chorisopora brongniartii* and left colony *Disporella hispida*, (scale bar= 2 cm).

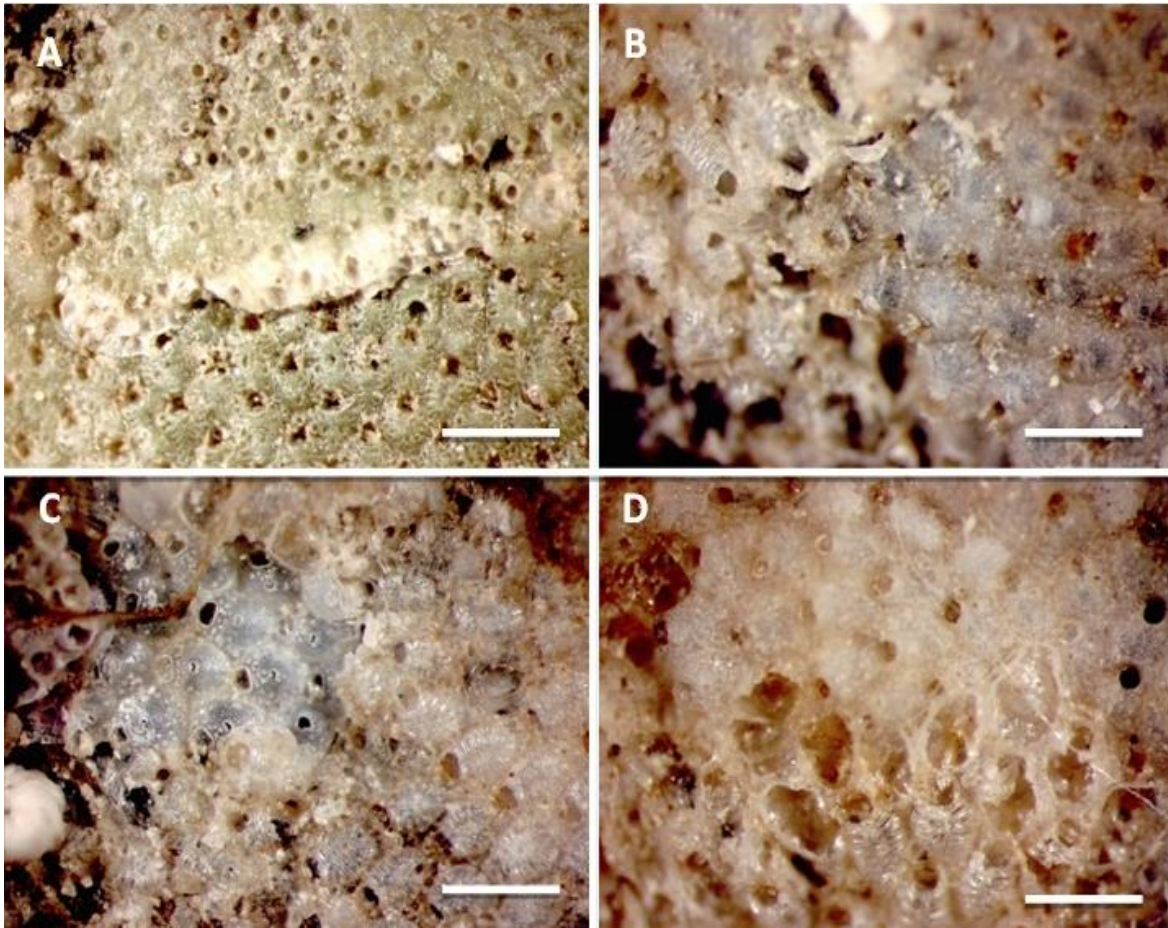


Figure 3.7: Noss Head, Scotland bryozoan species competitive interactions on horse mussel shells. A: overgrowth interaction between upper colony *Diplosolen obelia* (winning) and lower colony *Escharella immersa* (losing), (scale bar= 2.5 cm). B: overgrowth interaction between right colony *Escharella immersa* (losing) and left colony *Membraniporella nitida* (winning), (scale bar= 2 cm). C: overgrowth interaction between right colony *Membraniporella nitida* (winning) and left colony *Fenestrulina malusii* (losing), (scale bar= 2 cm), D: overgrowth interaction between upper colony *Schizomavella linearis* (losing) and lower colony *Membraniporella nitida* (winning), (scale bar= 2 cm).

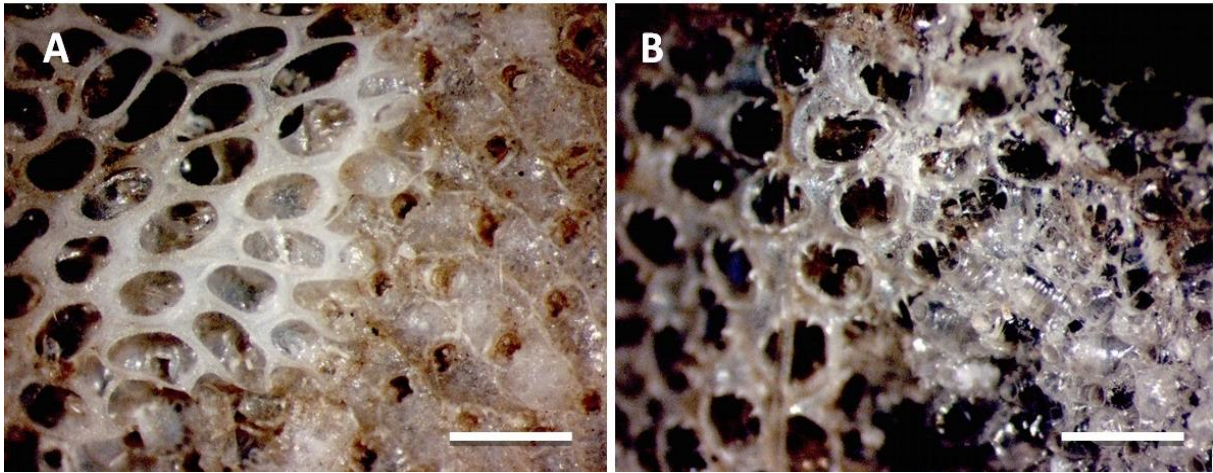


Figure 3.8: Dornoch Firth, Scotland bryozoan species competitive interactions in horse mussel's shells. A: overgrowth interaction between right colony *Escharella immersa* (losing) and left colony *Conopeum reticulum* (winning), (scale bar= 2 cm). B: overgrowth interaction between right colony *Celleporella hyalina* (losing) and left colony *Electra pilosa* (winning), (scale bar= 1.5 cm).

3.4.2. Shell region data analysis

Horse mussels shells from Noss Head site had the highest number of bryozoan competitive interactions, (393) followed by the Ramsey Bay (169), similar numbers in North Llyn (133), and lower numbers Dornoch Firth (44), Port Appin (40), Skarnsundet West Bridge (39), and Karlsruhe wreck (29). Bryozoan competitive interactions were higher in the posterior region of the shells than the anterior region across all sites. No interactions were observed in Loch Creran site as shown in Table 3.1.

Table 3.1: The number of bryozoan competitive interactions in horse mussel shell regions in each site (shells number =203).

Site	Interactions in posterior region	Interactions in anterior region
Isle of Man	111	61
Orkney	18	11
Norway	36	4
North Llyn	110	24
Port Appin	31	11
Loch Creran	-	-
Noss Head	255	138
Dornoch	34	10

Univariate analyses using a Chi-Square test revealed that there were statically significant differences in bryozoan competitive interactions between the posterior and anterior regions ($p < 0.001$, $n = 203$).

3.4.3. Competitive interaction types data analysis

Types of competitive interactions between bryozoan species were observed on horse mussel shells. Combined site data showed a high number in standoff interaction between bryozoan species. The number of standoff interactions was higher in Ramsey Bay, Karlsruhe wreck, Skarnsundet West Bridge, Port Appin and Dornoch Firth sites, while overgrowth interaction was higher in Noss Head and North Llyn sites. The number of fouling interactions was low in all sites and reciprocal interaction was only recorded in Noss Head site (Figure 3.9, Appendix H).

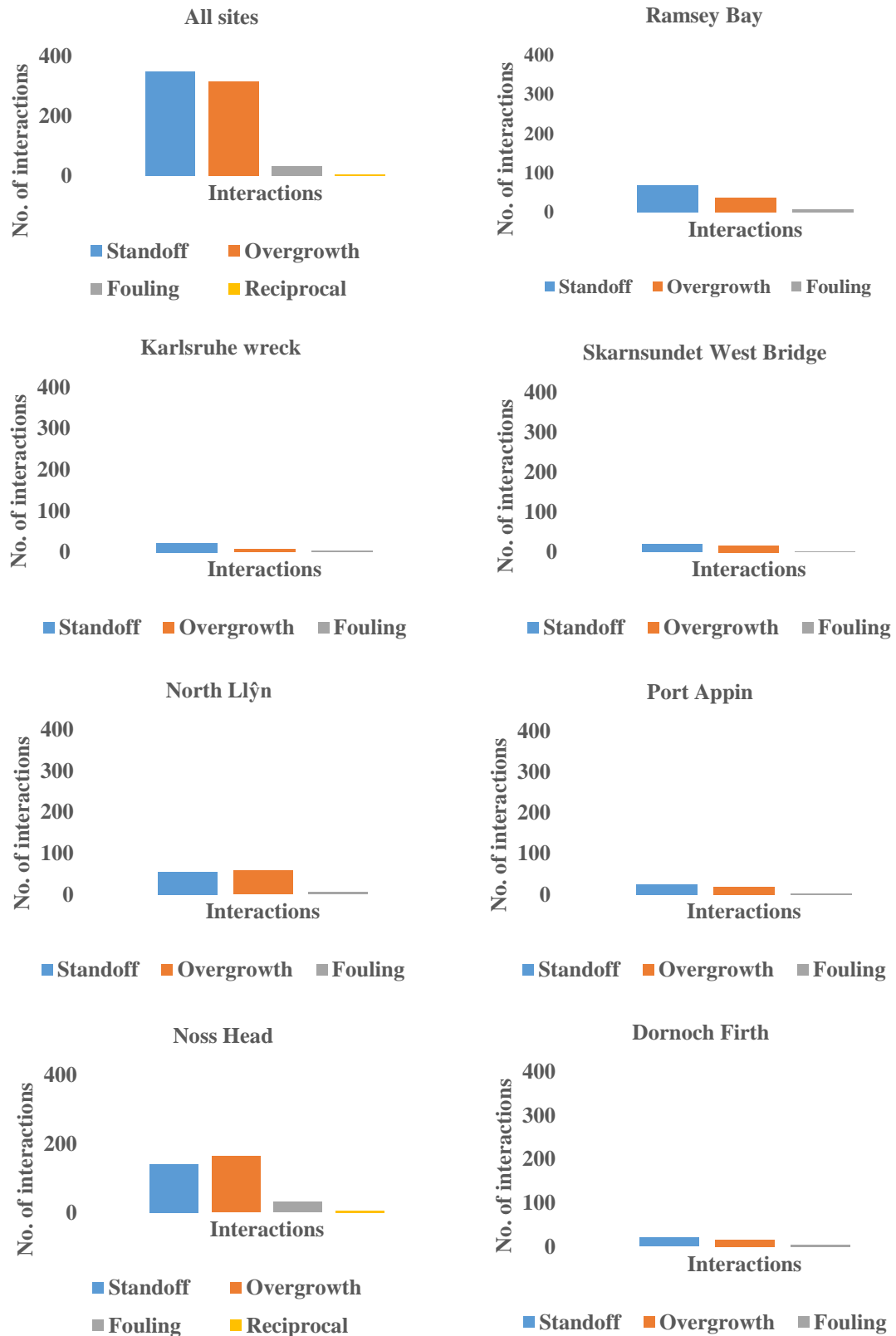


Figure 3.9: Number of competitive interaction types in all sites and in each individual site; standoff interaction was higher in all sites except in Noss Head and North Llŷn. Fouling was low in all sites and reciprocal interaction was only recorded at Noss Head.

ANOSIM analyses of similarity based on 9999 permutations showed that there are significant differences between the bryozoan species that fall into each of the competitive interaction types (Global R=0.046 and significance level: 0.1%), with the exception that fouling did not differ from reciprocal (Table 3.2).

Table 3.2: R values and significance of pairwise comparisons from analyses of similarities (ANOSIM) based on 9999 permutations in bryozoans competitive interactions types (significant differences in bold).

R values	Winning	Losing	Standoff	Fouling
Losing	0.005			
Standoff	0.02	0.014		
Fouling	0.03	0.048	0.124	
Reciprocal	0.056	0.082	0.196	-0.002
Significance%				
Losing	2.1			
Standoff	0.1	0.1		
Fouling	0.1	0.1	0.1	
Reciprocal	0.1	0.1	0.1	54.2*

* Not significant

SIMPER analysis highlighted key bryozoan species in the competitive interaction types (Table 3.3-3.11). In an overgrowth interaction the abundance of four bryozoan species *Diplosolen obelia*, *Patinella verrucaria*, *Escharella immersa*, and *Microporella ciliata* were always higher in the losing group except *Escharoides coccinea* which was always higher in the winning group (Table 3.3).

Bryozoan species abundance was higher in standoff interaction than winning and losing (Table 3.4, and 3.5). Fouling had lower bryozoan species abundance than winning, losing and standoff integrations (Table 3.6, 3.7, and 3.8). Reciprocal interaction also had lower bryozoan species abundance than winning, losing and standoff interaction (Table 3.9, 3.10, and 3.11).

Table 3.3: Average abundance of bryozoan species in winning and losing competitive interaction provided by SIMPER analysis (average dissimilarity = 95.14).

Species	Winning group Av.Abund	Losing group Av.Abund	Contribution%	Cumulative%
<i>Diplosolen obelia</i>	0.15	0.24	13.13	13.13
<i>Patinella verrucaria</i>	0.10	0.17	12.47	25.61
<i>Escharella immersa</i>	0.14	0.17	10.78	36.39
<i>Microporella ciliata</i>	0.09	0.10	9.37	45.76
<i>Escharoides coccinea</i>	0.16	0.09	6.33	52.09

Table 3.4: Average abundance of bryozoan species in winning and standoff competitive interaction provided by SIMPER analysis (average dissimilarity = 94.33).

Species	Winning group Av.Abund	Standoff group Av.Abund	Contribution%	Cumulative%
<i>Escharella immersa</i>	0.14	0.38	12.12	12.12
<i>Diplosolen obelia</i>	0.15	0.27	10	22.55
<i>Microporella ciliata</i>	0.09	0.24	43	32.36
<i>Patinella verrucaria</i>	0.10	0.22	9.81	40.78
<i>Escharoides coccinea</i>	0.16	0.13	8.42	46.62
<i>Schizomavella linearis</i>	0.10	0.15	5.85	52.39

Table 3.5: Average abundance of bryozoan species in losing and standoff competitive interaction provided by SIMPER analysis (average dissimilarity = 93.44).

Species	Losing group Av.Abund	Standoff group Av.Abund	Contribution%	Cumulative%
<i>Escharella immersa</i>	0.17	0.38	12.31	12.31
<i>Diplosolen obelia</i>	0.24	0.27	12.24	24.55
<i>Patinella verrucaria</i>	0.17	0.22	10.59	35.14
<i>Microporella ciliata</i>	0.10	0.24	9.58	44.71
<i>Electra pilosa</i>	0.08	0.13	5.69	50.40

Table 3.6: Average abundance of bryozoan species in winning and fouling competitive interaction provided by SIMPER analysis (average dissimilarity = 98.09).

Species	Winning group Av.Abund	Fouling group Av.Abund	Contribution%	Cumulative%
<i>Diplosolen obelia</i>	0.15	0.08	11.48	11.48
<i>Patinella verrucaria</i>	0.10	0.06	11.04	22.52
<i>Escharella immersa</i>	0.14	0.03	9.98	32.50
<i>Escharoides coccinea</i>	0.16	0.09	9.50	42.00
<i>Microporella ciliata</i>	0.09	0.01	8.88	50.88

Table 3.7: Average abundance of bryozoan species in losing and fouling competitive interaction provided by SIMPER analysis (average dissimilarity = 97.86).

Species	Losing group Av.Abund	Fouling group Av.Abund	Contribution%	Cumulative%
<i>Patinella verrucaria</i>	0.17	0.06	16.23	16.23
<i>Diplosolen obelia</i>	0.24	0.08	15.74	31.97
<i>Escharella immersa</i>	0.17	0.03	10.09	42.06
<i>Microporella ciliata</i>	0.10	0.01	8.05	50.11

Table 3.8: Average abundance of bryozoan species in standoff and fouling competitive interaction provided by SIMPER analysis (average dissimilarity = 97.92).

Species	Standoff group Av.Abund	Fouling group Av.Abund	Contribution%	Cumulative%
<i>Escharella immersa</i>	0.38	0.03	12.78	12.78
<i>Diplosolen obelia</i>	0.27	0.08	11.13	23.91
<i>Microporella ciliata</i>	0.24	0.01	9.43	33.34
<i>Patinella verrucaria</i>	0.22	0.06	8.91	42.25
<i>Escharoides coccinea</i>	0.13	0.09	5.45	47.70
<i>Schizomavella linearis</i>	0.15	0.01	4.74	52.44

Table 3.9: Average abundance of bryozoan species in winning and reciprocal competitive interaction provided by SIMPER analysis (average dissimilarity = 98.50).

Species	Winning group Av.Abund	Reciprocal group Av.Abund	Contribution%	Cumulative%
<i>Diplosolen obelia</i>	0.15	0.10	14.22	14.22
<i>Escharella immersa</i>	0.14	0.02	10.83	25.06
<i>Microporella ciliata</i>	0.09	0.00	9.49	34.54
<i>Patinella verrucaria</i>	0.10	0.00	9.27	43.81
<i>Escharoides coccinea</i>	0.16	0.04	9.16	52.97

Table 3.10: Average abundance of bryozoan species in losing and reciprocal competitive interaction provided by SIMPER analysis (average dissimilarity = 98.25).

Species	Losing group Av.Abund	Reciprocal group Av.Abund	Contribution%	Cumulative%
<i>Diplosolen obelia</i>	0.24	0.10	18.79	18.79
<i>Patinella verrucaria</i>	0.17	0.00	15.39	34.18
<i>Escharella immersa</i>	0.17	0.02	10.90	45.08
<i>Microporella ciliata</i>	0.10	0.00	8.53	53.61

Table 3.11: Average abundance of bryozoan species in standoff and reciprocal competitive interaction provided by SIMPER analysis (average dissimilarity = 98.52).

Species	Standoff group Av.Abund	Reciprocal group Av.Abund	Contribution%	Cumulative%
<i>Escharella immersa</i>	0.38	0.02	13.58	13.58
<i>Diplosolen obelia</i>	0.27	0.10	12.90	26.48
<i>Microporella ciliata</i>	0.24	0.00	9.89	36.37
<i>Patinella verrucaria</i>	0.22	0.00	7.67	44.04
<i>Escharoides coccinea</i>	0.13	0.04	4.85	48.89
<i>Electra pilosa</i>	0.13	0.00	4.67	53.55

Diversity indices showed that total bryozoans' species (S) and individual's numbers (N) were higher in the standoff interaction and double that in winning interaction (Table 3.12).

Table 3.12: North-East Atlantic horse mussel shell diversity indices within types of bryozoans competitive interaction (number of shells =203).

Competitive interaction	Total Species (S)	Total individuals (N)	Species richness (d)	Pielou's evenness (J)	Shannon Wiener diversity (H[Loge])	Simpson's diversity (1-Lamda)
Winning	28	1.5	62.3	0.8	2.8	2.6
Losing	26	1.7	45.8	0.8	2.6	2.1
Standoff	32	3.5	24.6	0.8	2.9	1.2
Fouling	24	0.5	0.0	0.8	2.6	0.0
Reciprocal	5	0.2	0.0	0.8	1.3	0.0

3.4.4. Size frequency data analysis

ANOSIM analyses of similarity based on 9999 permutations showed that there are differences between the shell size classes in relation to overall level of competition (Global R= 0.015 and significance level: 0.1%). The four smallest size classes (30-34.9, 35-39.9, 40-44.9, 45-49.9) were always significantly different from the two larger size classes (60-64.9, 65-69.9). Also (40-44.9, 45-49.9) were always significantly different from the four larger size classes (50-54.9, 55-59.9, 60-64.9, 65-69.9) as shown in Table 3.13.

Table 3.13: R values and significance levels for pairwise comparisons of analyses of similarities (ANOSIM) based on 9999 permutations in North-East Atlantic horse mussel's shell size classes in relation to competition (significant differences in bold).

R values	30-34.9	35-39.9	40-44.9	45-49.9	50-54.9	55-59.9	60-64.9
35-39.9	-0.024						
40-44.9	0.001	-0.04					
45-49.9	-0.012	-0.055	0.002				
50-54.9	0.019	-0.007	0.022	0.03			
55-59.9	0.013	-0.013	0.014	0.025	0		
60-64.9	0.046	0.035	0.028	0.042	0.011	0.007	
65-69.9	0.125	0.215	0.053	0.081	0.009	0.009	0.004
Significance%							
35-39.9	86.9*						
40-44.9	40.5*	98.8*					
45-49.9	81.2*	99.7*	26.8*				
50-54.9	1.5	62.9*	0.1	0.1			
55-59.9	9.8*	77.8*	0.4	0.1	43.8*		
60-64.9	0.1	3.2	0.5	0.1	5.1*	17.5*	
65-69.9	0.1	0.1	1	0.1	24.9*	27*	32.6*

* Not significant

SIMPER analysis highlighted the abundance of competing bryozoan species between the shell size classes (Table 3.14 – 3.25). Bryozoan species tend to compete more for space on horse mussel shells in the smaller size classes (30-34.9, 35-39.9, 40-44.9, 45-49.9) than in the larger size classes (50-54.9, 55-59.9, 60-64.9, 65-69.9). The species *Microporella ciliata* always competes more in the larger shell size classes.

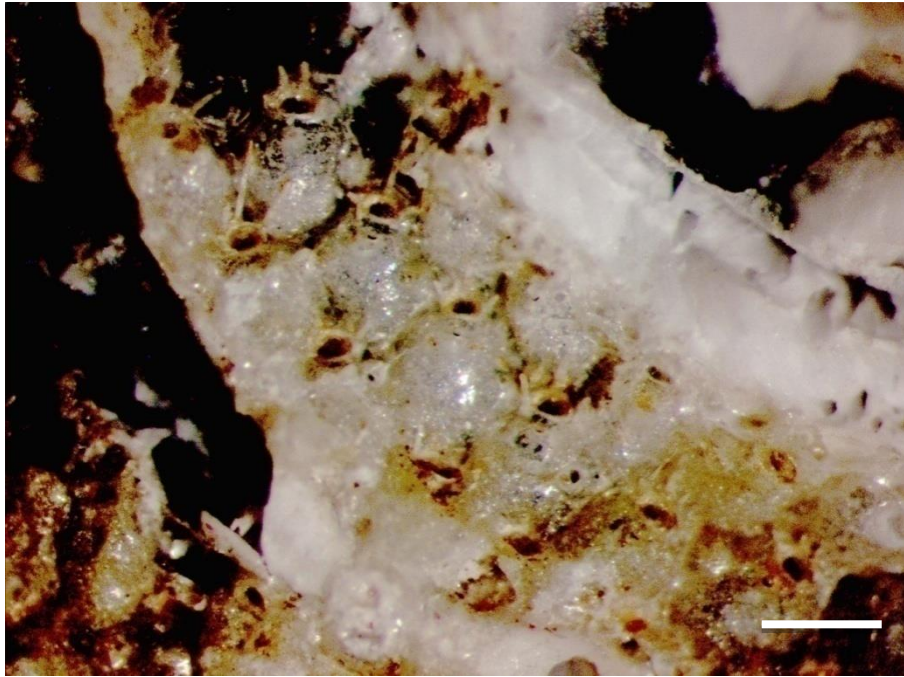


Figure 3.10: Bryozoan species *Microporella ciliata* settled between and above *Spirobranchus triqueter* tube worm on a horse mussel shell from the Isle of Man site, (scale bar = 2 cm).

Table 3.14: Differences in bryozoan species composition between shell size classes 30-34.9 and 60-64.9 mm analysed by SIMPER analysis (average dissimilarity = 95.44).

Species	30-34.9 Av.Abund	60-64.9 Av.Abund	Contribution%	Cumulative%
<i>Diplosolen obelia</i>	0.30	0.15	15.76	15.76
<i>Patinella verrucaria</i>	0.23	0.10	13.92	29.68
<i>Escharella immersa</i>	0.29	0.13	13.04	42.72
<i>Membraniporella nitida</i>	0.25	0.00	7.77	50.49

Table 3.15: Differences in bryozoan species composition between shell size classes 30-34.9 and 65-69.9 mm analysed by SIMPER analysis (average dissimilarity = 96.91).

Species	30-34.9	65-69.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Escharella immersa</i>	0.29	0.11	13.59	13.59
<i>Diplosolen obelia</i>	0.30	0.07	11.56	25.16
<i>Patinella verrucaria</i>	0.23	0.04	11.20	36.36
<i>Microporella ciliata</i>	0.05	0.19	9.62	45.98
<i>Membraniporella nitida</i>	0.25	0.00	8.04	54.02

Table 3.16: Differences in bryozoan species composition between shell size classes 35-39.9 and 60-64.9 mm analysed by SIMPER analysis (average dissimilarity = 95.25).

Species	35-39.9	60-64.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Diplosolen obelia</i>	0.51	0.15	20.00	20.00
<i>Escharoides coccinea</i>	0.43	0.00	11.86	31.87
<i>Patinella verrucaria</i>	0.26	0.10	11.02	42.89
<i>Membraniporella nitida</i>	0.30	0.00	8.71	51.59

Table 3.17: Differences in bryozoan species composition between shell size classes 35-39.9 and 65-69.9 mm analysed by SIMPER analysis (average dissimilarity = 97.52).

Species	35-39.9	65-69.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Diplosolen obelia</i>	0.51	0.07	17.49	17.49
<i>Escharoides coccinea</i>	0.43	0.00	12.09	29.58
<i>Membraniporella nitida</i>	0.30	0.00	8.91	38.48
<i>Patinella verrucaria</i>	0.26	0.04	8.65	47.14
<i>Schizomavella linearis</i>	0.35	0.00	8.05	55.19

Table 3.18: Differences in bryozoan species composition between shell size classes 40-44.9 and 50-54.9 mm analysed by SIMPER analysis (average dissimilarity = 96.64).

Species	40-44.9	50-54.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Patinella verrucaria</i>	0.08	0.12	12.05	12.05
<i>Diplosolen obelia</i>	0.20	0.11	11.13	23.17
<i>Microporella ciliata</i>	0.03	0.18	10.97	34.14
<i>Escharella immersa</i>	0.23	0.07	10.38	44.52
<i>Schizomavella linearis</i>	0.14	0.05	6.89	51.41

Table 3.19: Differences in bryozoan species composition between shell size classes 40-44.9 and 55-59.9 mm analysed by SIMPER analysis (average dissimilarity = 96.91).

Species	40-44.9	55-59.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Diplosolen obelia</i>	0.20	0.16	12.86	12.86
<i>Escharella immersa</i>	0.23	0.10	11.20	24.06
<i>Patinella verrucaria</i>	0.08	0.06	8.21	32.27
<i>Microporella ciliata</i>	0.03	0.14	8.19	40.46
<i>Escharoides coccinea</i>	0.15	0.06	6.88	47.34
<i>Schizomavella linearis</i>	0.14	0.00	5.25	52.59

Table 3.20: Differences in bryozoan species composition between shell size classes 40-44.9 and 60-64.9 mm analysed by SIMPER analysis (average dissimilarity = 96.76).

Species	40-44.9	60-64.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Diplosolen obelia</i>	0.20	0.15	13.76	13.76
<i>Escharella immersa</i>	0.23	0.13	11.85	25.61
<i>Patinella verrucaria</i>	0.08	0.10	10.45	36.07
<i>Schizomavella linearis</i>	0.14	0.01	5.89	41.95
<i>Tubulipora phalangea</i>	0.06	0.09	5.62	47.57
<i>Conopeum reticulum</i>	0.00	0.09	5.01	52.58

Table 3.21: Differences in bryozoan species composition between shell size classes 40-44.9 and 65-69.9 mm analysed by SIMPER analysis (average dissimilarity = 97.59).

Species	40-44.9	65-69.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Escharella immersa</i>	0.23	0.11	12.55	12.55
<i>Microporella ciliata</i>	0.03	0.19	10.12	22.67
<i>Diplosolen obelia</i>	0.20	0.07	8.49	31.16
<i>Conopeum reticulum</i>	0.00	0.14	7.84	39.00
<i>Patinella verrucaria</i>	0.08	0.04	6.73	45.72
<i>Schizomavella linearis</i>	0.14	0.00	5.12	50.85

Table 3.22: Differences in bryozoan species composition between shell size classes 45-49.9 and 50-54.9 mm analysed by SIMPER analysis (average dissimilarity = 96.09).

Species	45-49.9	50-54.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Diplosolen obelia</i>	0.26	0.11	13.60	13.60
<i>Patinella verrucaria</i>	0.17	0.12	13.22	26.82
<i>Microporella ciliata</i>	0.04	0.18	10.15	36.98
<i>Escharella immersa</i>	0.23	0.07	10.12	47.09
<i>Escharoides coccinea</i>	0.22	0.07	8.13	55.23

Table 3.23: Differences in bryozoan species composition between shell size classes 45-49.9 and 55-59.9 mm analysed by SIMPER analysis (average dissimilarity = 96.42).

Species	45-49.9	55-59.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Diplosolen obelia</i>	0.26	0.16	15.40	15.40
<i>Escharella immersa</i>	0.23	0.10	10.91	26.31
<i>Patinella verrucaria</i>	0.17	0.06	9.87	36.18
<i>Escharoides coccinea</i>	0.22	0.06	8.33	44.51
<i>Microporella ciliata</i>	0.04	0.14	7.38	51.90

Table 3.24: Differences in bryozoan species composition between shell size classes 45-49.9 and 60-64.9 mm analysed by SIMPER analysis (average dissimilarity = 96.23).

Species	45-49.9	60-64.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Diplosolen obelia</i>	0.26	0.15	15.97	15.97
<i>Patinella verrucaria</i>	0.17	0.10	11.76	27.72
<i>Escharella immersa</i>	0.23	0.13	11.57	39.29
<i>Escharoides coccinea</i>	0.22	0.00	6.32	45.61
<i>Tubulipora phalangea</i>	0.05	0.09	4.95	50.56


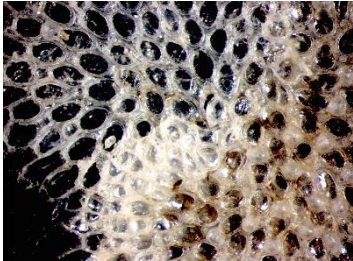

Table 3.25: Differences in bryozoan species composition between shell size classes 45-49.9 and 65-69.9 mm analysed by SIMPER analysis (average dissimilarity = 97.45).

Species	45-49.9	65-69.9	Contribution%	Cumulative%
	Av.Abund	Av.Abund		
<i>Escharella immersa</i>	0.23	0.11	12.16	12.16
<i>Diplosolen obelia</i>	0.26	0.07	11.37	23.53
<i>Microporella ciliata</i>	0.04	0.19	9.24	32.77
<i>Patinella verrucaria</i>	0.17	0.04	8.46	41.23
<i>Conopeum reticulum</i>	0.00	0.14	7.47	48.70
<i>Escharoides coccinea</i>	0.22	0.00	6.58	55.28

3.4.5. Karlsruhe wreck panels

Low numbers of bryozoan species colonization and competition interaction were observed on panels from Karlsruhe wreck site.

Table 3.26: Bryozoan competitive interactions on panels in Karlsruhe wreck site. (W: winning colony, L: losing colony).

Deployed	Retrieved	Type of interaction	Species
May 2014	12-9-2014	Standoff 	<i>Microporella ciliata</i> (upper colony) x <i>Microporella ciliata</i> (lower colony)
May 2014	21-6-2015	Overgrowth 	<i>Callopora lineata</i> (right colony) (W) x <i>Callopora lineata</i> (left colony) (L)
May 2014	21-6-2015	Standoff 	<i>Electra pilosa</i> (right colony) x <i>Microporella ciliata</i> (left colony)
12-2-2014	13-2-2015	No competitive interactions	-
13-2-2015	21-6-2015	No competitive interactions	-

3.5. Discussion

The overall aim of this study was to investigate competitive interactions of sessile epifaunal cover on the shells of horse mussel *Modiolus modiolus* from eight horse mussel beds throughout the geographical range of the species.

3.5.1. Shell region

The number of bryozoan competitive interactions was higher in the posterior region than the anterior region of the shells across all sites as shown in Table 3.1. This might be due to food availability produced by the feeding currents from horse mussels siphons on the posterior region of the shell (Dinesen and Morton, 2014). Species competition for space during early community development would be expected to be higher at the specific part of the substrate where growing conditions are more favourable because many marine epifaunal organisms are suspension feeders (Maughan and Barnes, 2000). Dobretsov and Wahl (2008) reported that invertebrate larvae of bryozoans can reject or accept the substrate in response to the water flow, in which it reached the substrate via the current and settle if the surface is suitable for colonization or it will de-attach from the surface and return to the water column. Re-entering the water column allows larvae to search over a greater area, with the possibility of encountering better habitat; however, there are the risks of mortality in the plankton or not encountering other settlement habitat (Burgess et al., 2009). A study by Walters et al. (1999) observed, recorded and analyzed the larval behaviour of two sessile marine invertebrates, the barnacle *Balanus amphitrite* and the bryozoan *Bugula neritina* while settling on hard surfaces at various flow rates. They reported that larvae seek locations where attachment to the substrate is secure, predation and physical disturbances are minimized and food availability is greatest where flow rates are highest. Their results demonstrated that both flow rate and organisms previously recruited to the surface significantly influenced larval exploration and ultimately the selected settlement site.

3.5.2. Competitive interaction types

The number of standoff interaction between bryozoan colonies was proven to be statistically significantly higher than the number of overgrowth interactions. There are strong similarities between the above results and a study by Maughan and Barnes (2000) which investigated settlement panels immersed at Lough Hyne, County Cork, Ireland, and reported that half the interactions recorded were a standoff between *Microporella ciliata* and *Celleporella hyalina*. They suggested that this may be an adaptive competitive strategy for opportunistic species in

disturbed habitats (Maughan and Barnes, 2000). Marine habitats tend to be subjected to high levels of disturbances from both natural factors such as storm waves and sediment scour, and human activity factors such as building of bridges, offshore platforms, and marine energy installations (Airoidi and Bulleri, 2011). Opportunistic species generally colonize vacated space quicker than others, because of their fast growth and high recruitment rates. Many ecosystems possess multiple opportunistic species and many of these are relatively weak competitors. In highly disturbed systems, released space brings the opportunity for a number of species to rapidly grow and dominate (González-Rivero et al., 2015). In the current study, the sites experienced moderate to strong tidal flow conditions, as these hydrodynamic conditions are favourable to the growth of *Modiolus modiolus* (Hydrographic office, 1992, 2017a, 2017b).

Bryozoan larvae avoid overgrowth mortality by selective settlement of a weak competitive species away from competitive dominants. Large bryozoan colonies are able to suffer partial mortality without loss of the entire genetic individual but for small colonies mortality of few zooids in the initial stages of the colony growth would have a much more serious effect, such as killing off the ancestrula or feeding zooids by an overgrowth in young colonies, will affect the translocation of nutrients across the growing colony and inhibit colony growth (Rubin, 1985). Standoff interactions are the most common type and ecologically important since the frequency of standoff encounters are highly connected with the local scale biodiversity. A study by Barnes and Kuklinski (2005) investigated the dominance of standoff interactions between littoral and sub-littoral bryozoans at Spitsbergen, Svalbard, and in the Scotia Arc and Antarctic Peninsula. The study reported that patterns of standoff competition can be used as a signal of the extent of biological response to polar ocean warming and glacier collapses which might lead to a decrease in patchiness, and an increase in the abundance of standoff competition (Barnes and Kuklinski, 2005). Karlson (1980) suggested that standoff interactions between colonial species are a defensive strategy and might be a successful way to restore disturbed habitats in which bare substratum generated by physical disturbance provides growth opportunities for species relies on a standoff strategy.

Fouling interaction had lower bryozoan species abundance than overgrowth and standoff integrations which could be due to some of the interactions of fouling species being species specific (Nandakumar and Tanaka, 1997). At the Karlsruhe wreck site *Escharella immersa* were always fouling over *Parasmittina trispinosa* in three separate interactions and in Noss

Head site five bryozoan species *Amphiblestrum flemingii*, *Membraniporella nitida*, *Smittoidea reticulata*, *Patinella verrucaria*, and *Cellepora pumicosa* were always recorded fouling over *Escharoides coccinea* species on different shells however the later was never recorded fouling over the former species. A study by Sellheim et al. (2010) reported that some epifaunal species have physical, mechanical or chemical means to expel and reject settlement of other sessile species, which can predict species-specific fouling interaction of sessile epifaunal communities.

Results of this study showed that the species *Escharoides coccinea* was always a winner in an overgrowth interaction, indicating that it is a strong competitor. In contrast, *Microporella ciliata* always loses in an overgrowth interaction, indicating that it is a weak competitor. These results are compatible with a similar study by Rubin (1982), where it was reported that bryozoan species have different competitive abilities.

3.5.3. Competitive interactions and latitude

Competitive interactions, productivity, habitat complexity, disturbance, and environmental stress influence local marine epifaunal species richness. But, local diversity must also be affected by regional-scale processes. A study by Witman, et al. (2004) investigated the latitudinal variation in species richness at both regional and local spatial scales from sites located in marine reserves (Galapagos Islands, Seychelles Islands, and Palau Islands), national parks (Eastern Caribbean and Norfolk Islands), or a biosphere reserve (New Zealand Fiords and Antarctica). Their analyses showed that regional enrichment of local marine diversity increased from low to high latitudes. They suggested that the effects of latitude on local diversity are expressed through variation in species interactions, habitat heterogeneity, and variation in recruitment. Witman et al. (2004) concluded that the number of species coexisting in local marine communities is influenced by the diversity of the regional species pool and is not determined only by small-scale ecological processes operating within communities.

Competition and disturbance have important influences on the structure and diversity of marine hard substratum communities (Barnes and Rothery, 1996). Barnes (2002) investigated if large-scale latitudinal patterns exist in the structure of benthic assemblage are due to competition and reported that recruitment and growth of sessile invertebrates are low in shallow polar benthic communities; however competition is a dominant process that influence assemblage structure after a disturbance. Disturbance in the polar marine environment is variable and occur through the action of ice scour. Barnes, (2002) suggested

that benthic communities diversity is maintained by the frequent nature of disturbance in Polar Regions, in which, without it a few species would outcompete all others and monopolize large areas of space.

3.5.4. Shell size

Results from this study showed that bryozoan species tend to compete more intensively for space on the smaller size classes of horse mussel shells. Availability of space can become a limiting factor for sessile epifaunal communities and may lead to intense competition between species in both standoff and overgrowth interactions. Polychaete species are strong competitors for space and may ultimately become dominant and overgrow and prevent space for faster growing bryozoans (Holloway and Keough, 2002). It was noticeable from the results that *Microporella ciliata* colonies were able to compete more successfully in the larger shell size classes. Rubin (1985) suggested that certain cheilostome bryozoans settle preferentially on polychaete worms, using their tubes as secondary space. Such a strategy might also improve competitive ability by raising their height above a competitor as well as avoid overgrowth interaction by escaping overgrowth mortality by growing regularly onto tubes of neighbouring *Spirobranchus triqueter* as seen in *Microporella ciliata* species in (Figure 3.10).

A study by Ramsfjell (2016) investigated the effect of Bryozoa zooid size on competitive interactions outcomes on the following species; *Antarctothoa tongima*, *Aimulosia marsupium*, *Arachnopusia unicornis*, *Microporella agonists* and *Crepidacantha crinispina*.

The study reported among all species, *Arachnopusia unicornis* colonies which had the biggest zooid size always won in overgrowth interactions.

The above finding contradicts this study's results mentioned in (Section 2.4.1. and Table 3.3). In an overgrowth interaction *Microporella ciliata* species was the weakest competitor and had a big zooid size, measuring within a range of 527.6 – 603.9 µm in length and 464 – 554.8 µm in width, while *Escharella immersa* was a stronger competitor but had a smaller zooid size, measuring within a range of 442.1 – 517.1 µm in length and 206.4 – 353.1 µm in width. These results might indicate that the relationship between bryozoan zooid size and winning in competition interaction differs between species.

3.5.5. Conclusion

The results of this study showed that bryozoan competition is largely found on the posterior region of the horse mussel shells. The assemblage is dominated by standoff interaction between bryozoan species; this is a strategy used to avoid mortality from overgrowth. Bryozoan species competition numbers decreased with the increase of horse mussel shell size in keeping with the decrease of bryozoan colonies with the increase of shell size (Figure 2.14). This study is an important step towards the understanding of the factors controlling competitive interactions of bryozoan species on horse mussels. Bryozoan colonial growth and competition have an important ecological role that can be used to analyse species abundance and richness and their distribution in horse mussel bed reefs.

3.5.6. Future studies

Future studies on other important factors for bryozoan survival could include: larval recruitment, colony growth rate, colony size, colony thickness and growth form. These types of studies are needed in order to understand the outcomes of competitive interactions between bryozoan species and ultimately, species coexistence in biogenic reef system. Artificial substrata such as panels could be used to provide surfaces for bryozoans that get checked monthly for species settlement and growth. An understanding of such epifaunal communities could also be important due to influxes of non-native species which may arrive and disrupt natural ecosystems. The impact of non native species cannot be fully quantified and understood, if the dynamics of natural systems are not fully understood. This is especially important in sensitive habitats such as biogenic reefs which have high conservation importance.

4. Chapter 4: Marine bryozoan diversity in coastal waters of Qatar

4.1. Introduction

4.1.1. Coastal waters of the Arabian Gulf

The Arabian Gulf is in South-western Asia and comprises an extension of the Indian Ocean through the Strait of Hormuz; it is located between Iran to the northeast and the Arabian Peninsula to the southwest, between longitudes 48°–56° E and latitudes 24°–30° N. The Arabian Gulf is a semi-open sea of 40,000 m² area (Vaezi et al., 2015). The southern and western portion of the Arabian Gulf is characterized by soft sediment and coral limestone habitats. Subtidal sediments consist of thin layers of relatively pure carbonate sands or mud over solid conglomerates. In areas with low currents, sand and shell gravel accumulate and form habitat for epifaunal and benthic organisms (Sale et al., 2011).

The Arabian Gulf harbours extensive coral reefs due to its latitudinal position, its shallow nature, and its position within the great desert belt (Figure 4.1). The Arabian Gulf and its coral reefs are exposed to extremes in temperature, salinity and other physical factors, but despite the extreme climate, coral habitats have shown a remarkable resilience to extreme environmental conditions (Riegl and Purkis, 2012). Summer daily surface water temperatures reach on average 33°C with the maximum often exceeding 36 °C. In winter time surface water temperature ranges from 16°C to 22°C with the lowest temperature reported as 11.5°C, with salinity observations as high as 45 EC (Sale et al., 2011). These observations show that coral reef faunal communities are capable of tolerating extreme sea temperatures.

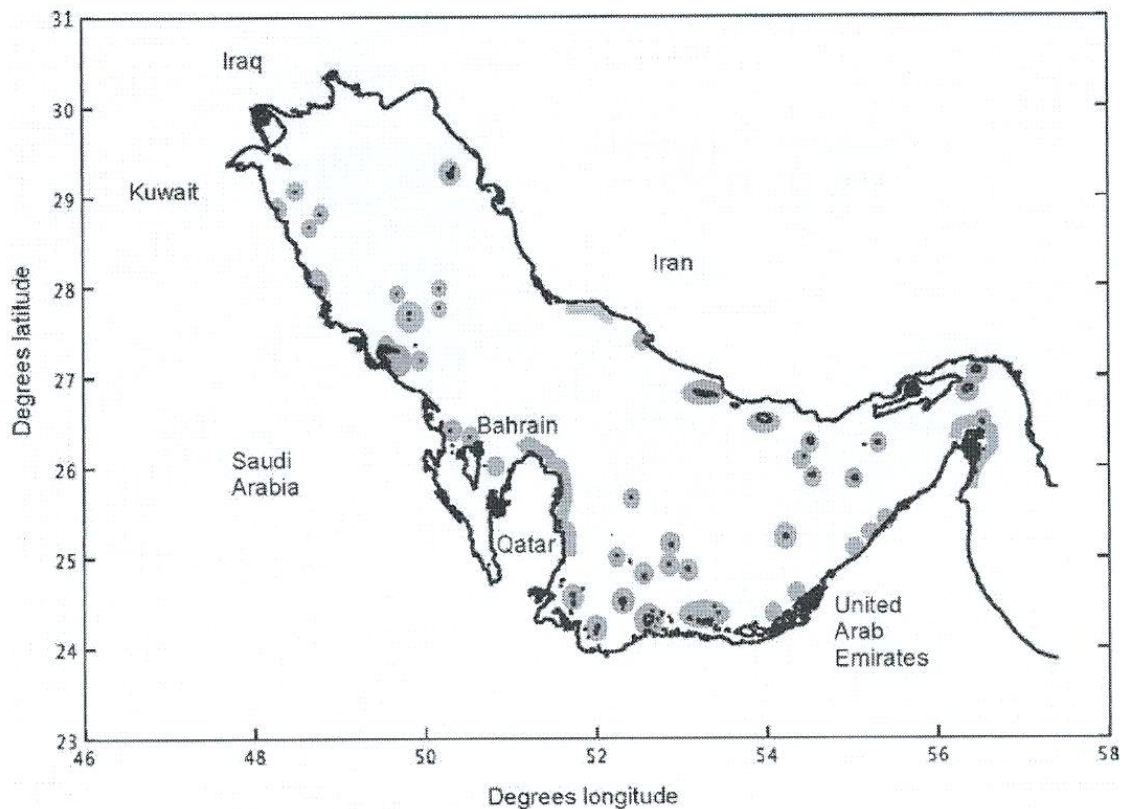


Figure 4.1: Locations of areas in the Arabian Gulf with extensive coral growth are indicated by grey lines (Riegl and Purkis, 2012).

The Arabian Gulf has extensive fishing grounds, coral reefs, and abundant pearl oyster beds. There is an increased interest in the development of new research programs within the Arabian Gulf region to understand the importance of physical extremes in the structure of coral reefs and pearl oyster habitats and associated biological communities. Most research on coral reef communities within the Gulf has historically been based around baseline assessments, usually associated with large-scale coastal development projects. However, recent research has begun to focus on understanding mechanisms important in the ecological structure and function of marine communities (Feary et al., 2013).

Atmospheric circulation patterns in the Arabian Gulf are influenced by the Indian Ocean monsoon and the dominant wind direction is usually from North-West towards South-East, which makes the environment in the South-East region of the Gulf the most exposed sediments that occur to depth of about 20m, and the North-West region the most sheltered. North-West winds called ‘Shamal’ are the most important weather patterns that occur most dramatically during winter than in summer. During ‘Shamal’, the Arabian Gulf experiences strong force winds, with the stronger winds and larger swells in the Southern portion than the

Northern portion due to fetch limitations. The highest wave magnitude occurs near the regions of North-East cost of the Qatar Peninsula, and Lavan Island in Iran, as illustrated in Figure 4.2 (Riegl and Purkis, 2012).

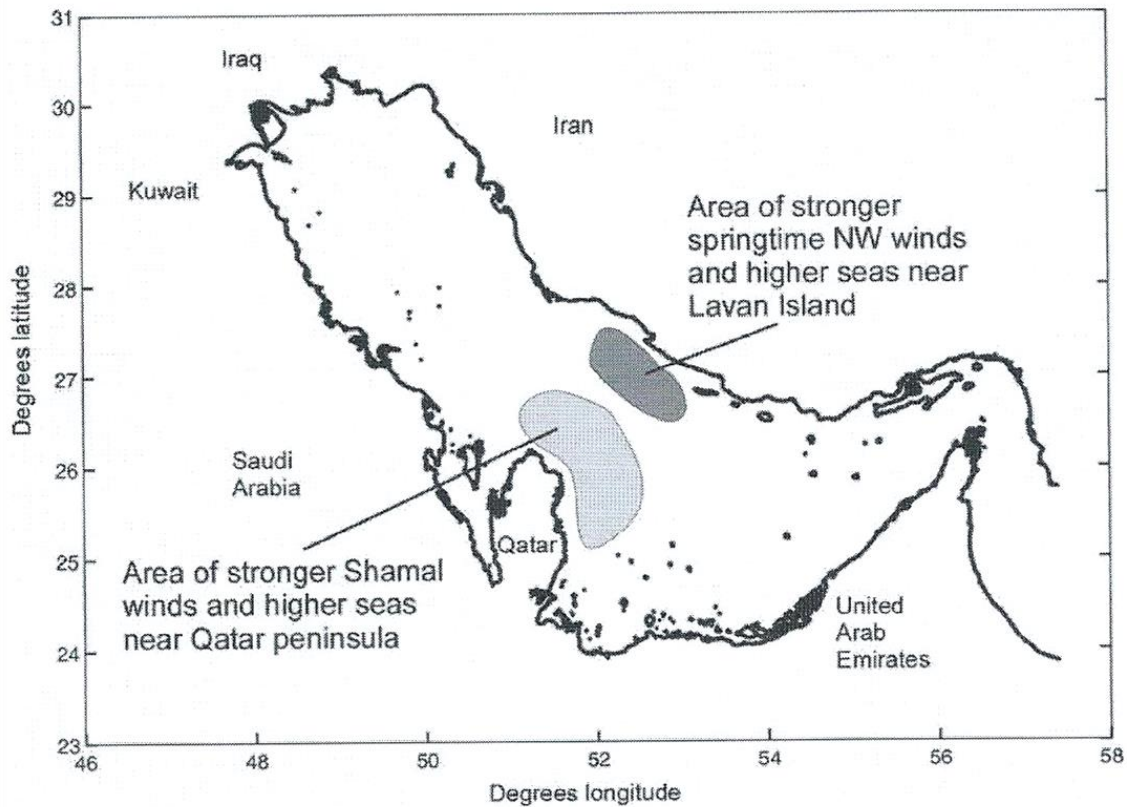


Figure 4.2: Arabian Gulf areas of strong force winds and occurrence of high waves (Riegl and Purkis, 2012).

4.1.2. Coastal waters of Qatar

Qatar is located halfway along the western coast of the Arabian Gulf, between latitude $24^{\circ} 40' 26'' 10''\text{N}$ and longitude $50^{\circ} 45' 51'' 40''\text{E}$ and covers an area of about $28,000 \text{ km}^2$. Depths of the coastal waters are generally shallow and range between 10 and 60 meters. The coastal environment around Qatar is exposed to land based as well as marine activities including oil loading and unloading, oil fields, industrial parks, harbours, coastal structures, dredging, and sewage, all of which have negative impacts on the marine environment (Ahmed and Abdel-Moati, 2003). Grain size analysis showed that Qatar is dominated by sand sized sediments. The sediments consist of a mixture of rough sand, medium to fine sand, and silt. Mean grain size ranged from a minimum of 1.34mm to a maximum of 3.86mm with an average of 2.50 mm. Silt content of the fine sandy deposits increased with increasing depth. Rocky bottoms,

submerged beach rocks and reef banks, are found along the near shore areas of Qatar (Ahmed and Abdel-Moati, 2003).

4.1.3. Coral reefs of the Arabian Gulf and Qatar

Coral reefs are one of the most diverse ecosystems in the marine environment. They are important in tropical countries and coastal areas by providing economically important services and products such as food, tourism revenue, as well as coastal protection (Feary et al., 2013). Coral reef communities in the Arabian Gulf are low in diversity and dominated by tolerant hard coral taxa such as *Favidae* and *Porites*. In the Arabian Gulf region, corals are described as coral carpets because they do not form true reefs; where individual colonies grow on exposed rocky substrates than building on older dead coral skeletons. These coral reefs are common in the southern region of the Arabian Gulf that is characterised by extreme and high sea surface temperature causing the reef to die-off on a regular basis which prevents the formation of a true reef building framework (Sale, 2011; Burt et al., 2014).

Despite the rapid growth in the field of coral reefs ecosystems in recent years, there is still a lack of knowledge regarding the biodiversity of coral reefs in the Arabian Gulf. The majority of reef studies in the Arabian Gulf assess the state of the reefs by recording the percentage coverage of major benthic organisms and by examining coral colony taxonomy and size-frequency distributions (Feary et al., 2013; Burt et al., 2014). An example includes the study by Al-Ansi and Al- Khayat (1999) who investigated the diversity of coral reefs and its associated biota along the eastern coast of Qatar. The study reported 17 coral species; *Stylophora pistillata*, *Acropora clathrata*, *Acropora* sp., *Montipora copricornis*, *Porites compressa*, *Goniopora lobbata*, *Alvepora* sp., *Favia* sp., *Favites pentagona*, *Goniastrea* sp., *Platygyra daedalea*, *Turnbinaria peltata*, *Dendrophyllia* sp., *Tubastraea*, *Echinopora* sp., *Echinophyllia* sp. and *Cirrihipathidae anguina*. The associated biota was dominated by molluscs settling on dead corals or on the upper surface of corals reefs. However, few bryozoan species were reported and included four species of the class Gymnolaemata; *Zoobotryon* sp., *Bugula* sp., *Schizoporella errata*, and *Watersipora subovidea*. To our knowledge this is the first published study of bryozoans from Qatar.

There has been a novel study by Burt et al. (2014) on the symbiotic relationships between corals and the algae zooxanthellae that live within the cell walls and provide energy for the growth and survival of corals. This study mainly focused on molecular biology/physiology to identify the mechanisms that allow coral reef to survive in the extreme conditions of the

Arabian Gulf. The study investigated coral reef sites along the coasts of United Arab Emirates and Oman, through the Strait of Hormuz and into the Arabian Sea. Genetic analysis showed that the thermal tolerance in the brain coral *Platygyra daedalea* and its zooxanthellae are unique to the Arabian Gulf. The alga was a novel species and was named *Symbiodinium thermophilum* due to its ability to withstand the high temperatures of the Arabian Gulf (Casey, 2015).

Experimental and field observations indicate that effects of high temperatures and ocean acidification could increase the frequency of bleaching and reduce coral calcification and since the majority of hard corals in the Arabian Gulf do not build true reef frameworks, they could be threatened by a shortage of suitable habitat. There have been major changes to southern Arabian Gulf coral reefs during the period 1996 and 1998 mass bleaching which increased the abundance and diversity of sessile invertebrate groups such as sponges, tunicates, and sea urchin growing on top of coralline algal covered dead coral, as well as seaweeds replacing hard corals. Also there was an increase in yellow-bar angelfish abundance (Feary et al., 2013). The rapid degradation and loss of the Arabian Gulf unique and important coral reef ecosystem has led to urgent improved regulation and management. Some Gulf countries such as Kuwait and Qatar have set multidisciplinary approaches including marine civil engineers, oceanographers, architects and biologists to limit the negative environmental impacts of certain coastal developments (Burt et al., 2014).

There was a first of its kind three years combined project between the Environment Agency Abu Dhabi (EAD) in the United Arab Emirates and Qatar's Supreme Council for the Environment and Natural Resources (SCENR) to monitor coral reefs, along Abu Dhabi's and Qatar's territorial waters and to develop a long-term conservation management plan for these coral reef habitats. The project also included the mapping of coral using satellite imagery and fieldwork around the islands (Abdul-Kader, 2008).

A project between the Qatar Ministry of Environment and the University of Qatar planted 500 pieces of coral along the coastline of Sealine Beach to protect the marine environment from degradation and provide an attractive environment to tourists (The Peninsula, 2011).

4.1.4. Pearl oyster reefs of the Arabian Gulf and Qatar

Molluscs are the most important sediment producers in the Arabian Gulf and Qatar due to their high population densities in sub-tidal and intertidal which make up the shallow sands

that often develop into hard grounds (Riegl and Purkis, 2012). Pearl oysters form vast beds in the western side of Arabian Gulf that extend from the Kuwaiti coast in the north to the coast of the United Arab Emirates and Oman in the south. Qatar and other Arabian Gulf countries had huge pearl oyster resources which were exploited for natural pearls as their main economic resources. The pearl oyster fishing industry in the Arabian Gulf declined with the development of cultured pearls in Japan during the 1930s and with the discovery of oil in the Gulf countries from 1900s to the 1980s (Al-Khayat and Al-Ansi, 2008). Qatar waters are rich in pearl oyster beds with the presence of different species of pearl oysters. *Pinctada radiata* (Leach, 1814) represents about 95% of the total oyster catch, while *Pinctada margaritifera* (Linnaeus, 1758) and *Pteria marmorata* represents about 5% (Mohammed and Yassien, 2003). In Qatar the pearl oyster *Pinctada radiata* has been used as a bio-indicator for metal pollution monitoring programmes in the Arabian Gulf environment since pearl oysters have long life spans, a good response to wide range of environmental changes and are abundant under favourable conditions facilitating quantitative analysis (Al-Madfa et al., 1998).

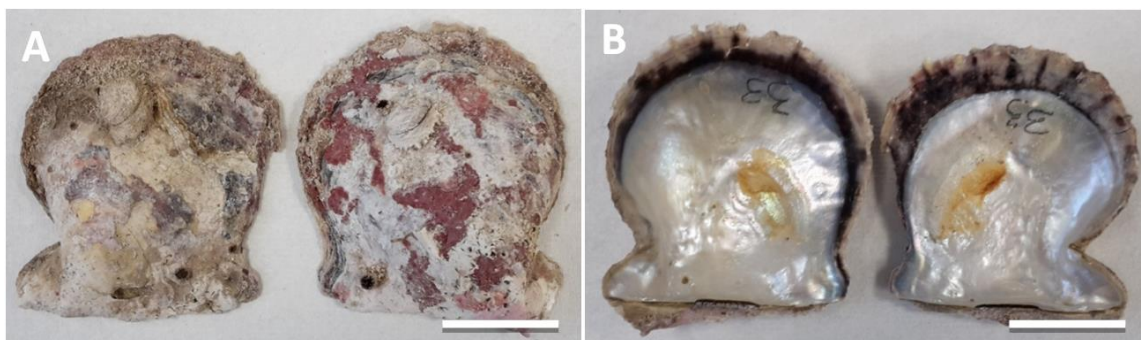


Figure 4.3: Pearl oyster *Pinctada radiata* from Qatar waters. A: shell outer surface (scale bar= 13.5 cm), B: shell inner surface (scale bar= 13.5 cm).

Pinctada radiata provide hard substrates for various epifaunal marine organisms such as echinoderms, crustaceans, corals, algae, polychaetes, and bryozoans. The epifaunal communities of pearl oyster beds, distribution abundance, topographical features, and general ecology as well as community structure and habitat conditions still remain generally poorly characterised (Wronski, 2010).

4.1.5. Pearl oyster *Pinctada radiata* description

Adult *Pinctada radiata* (Figure 4.3) have a fragile, thin and compressed, small to medium size shell usually 50-65 mm. The shell is inequivalve with the left valve more inflated, and has an almost quadrate outline. The dorsal margin is longer than the body of the shell. The

posterior margin is slightly concave and protrudes beyond the tip of the anterior ear. The beak points anteriorly, and the hinge line is straight with no teeth. The ligament is set in a single triangular depression. The external colour of the shell is variable. It can be uniform or with darker markings on radial rays, and is usually brownish or reddish. The outer surface has dense flattened concentric lamellae, with small radially projecting spines, mostly towards the margins. The internal side has a highly iridescent nacreous area, whereas the non-nacreous margin is glossy and light brown in colour, usually with dark brown or reddish blotches corresponding to the main external rays (Zenetos et al., 2004). *Pinctada radiata* are usually found attached to rocks, dead corals and various submerged objects, often forming large natural banks. They are common on sub-littoral bottoms from depths of 5 to 25 m. *Pinctada radiata* has a wide distribution found in both hemispheres and in most oceans and seas around the world. It is present in the Atlantic, Pacific and Indian oceans, the Arabian Gulf, the Red Sea, and more recently discovered in the Mediterranean Sea (Zenetos, 2016).

4.1.6. Marine Bryozoa of Qatar

Bryozoans have not been studied to any degree in the Qatar waters and there are no substantial base line data for this phylum to date. There have been several studies on marine benthic communities in the Arabian Gulf, mainly those of the intertidal coastal areas of Saudi Arabia, Kuwait, Bahrain and UAE (Al-Khayat, 1997). However, the benthic communities' composition, distribution, seasonal abundance and population size in Qatar are poorly characterised. The first record of a bryozoan species from Qatar was reported by Al-Ansi and Al-Khayat (1999), followed by Al-Khayat and Al-Maslamani (2001) who reported that *Schizoporella errata* is an important fouling organism, because its colony forms broad laminar encrustations on shells of the pearl oyster *Pinctada radiata*.

4.1.7. Skeletal mineralogy of bryozoans

Marine bryozoans precipitate calcium carbonate to form their skeletons, and they have evolved through both icehouse periods when aragonite was more precipitated in the sea, and green house periods when calcite was the favoured polymorph. Bryozoan Cheilostomata evolution has been driven by changes in seawater chemistry over time. Changes in the magnesium/calcium ratio in seawater have affected skeletal mineralogy of evolving bryozoan families, providing selective pressure resulting in a wide range of carbonate skeletal mineralogy seen in bryozoans today (Smith et al., 2006). Cheilostome bryozoans are active

controllers of bio-minerals in contrast to corals which have a limited ability to control bio-mineralization (Ries, 2009).

Bryozoans are composed of zooids that include inorganic skeleton and organic components such as cuticle and polypide. The bryozoan skeleton is secreted beneath the cuticle that is deposited by epithelial cells. The polypide includes the nervous system, digestive tract, muscles and the feeding apparatus lophophore (Lombardi et al., 2011). Calcification in a simple cheilostome bryozoan begins after cell differentiation. The process begins by the release of calcium ions into intracellular spaces, followed by the impregnation of an organic matrix with calcium salts. The build-up of calcium in the cuticular matrix occurs before any crystallization takes place. The precipitation of aragonite or calcite is determined either by the amino acid composition of the cuticle, or by ions present in the intercellular fluids. At the colony scale, basal walls are formed first from the proximal part of the zooid, with marginal walls following and the frontal shield last (Smith, 2014).

Marine bryozoans from the class Gymnolaemata show a wide range of mineralogies in their skeletal carbonate; dominance of calcite, the addition of aragonite in secondary calcification, the presence of entirely aragonitic bryozoans, the presence of bimineralic forms in which a calcite skeleton is later covered by aragonite (Taylor et al., 2016), and the presence of two distinct calcites (low-Mg calcite and dominant high-Mg calcite) (Smith et al., 2006).

Studies on skeletal mineralogy of marine bryozoans have been conducted on species from different geographical regions (McNeil et al., 2004; Cocito and Lombardi, 2012). Bryozoans are well suited to investigate the effects of extreme seawater chemistry on marine invertebrate evolution and development. Environmental and temporal variations of Qatar bryozoans cannot be interpreted without a clear understanding of the mineralogical variability present within the phylum. This study seeks to review our knowledge of Qatar bryozoan calcification and how they endure extreme ocean climate, particularly rising temperatures and salinity. By understanding how calcified organisms such as bryozoans are able to live in the naturally extreme conditions of the Arabian Gulf, it may be possible to predict the impacts of changes in seawater chemistry, as other regions start to experience more extreme conditions due to climate change.

4.2. Aim and objectives:

The aim of this study is to document the biodiversity and skeletal mineralogy of Bryozoa from coastal waters of Qatar. Objectives of the study are:

1. To conduct site surveys and collect samples by SCUBA during a research cruise along the coast of Qatar from coral and oyster reef habitats.
2. Identify and describe the species of marine Bryozoa using scanning electron microscopy.
3. Quantify the biodiversity of the Bryozoa fauna using PRIMER v7 software.
4. Determine the skeletal mineralogy of Qatar bryozoan species Mol. % MgCO_3 in calcite using X-ray Diffraction analysis.
5. Discuss the implications of these findings in relation to the extreme environmental conditions in the Arabian Gulf.

4.3. Material and methods

4.3.1. Fieldwork

As part of a research cruise aboard RV *Janan*, samples of marine Bryozoa were collected from Qatar waters; Samples were associated with pearl oysters *Pinctada radiata* and coral rubble. A total of 168 samples (coral rubble, shells, hydroids, sea fan and sand dollar) were collected from six stations along the coastline of Qatar from areas close to Doha and then at intervals northwards to Raslaffan (Figure 4.4). Environmental information for each station sampled was recorded for habitat description (Appendix I). Site location information is provided in Table 4.1 and illustrated in Figure 4.5.

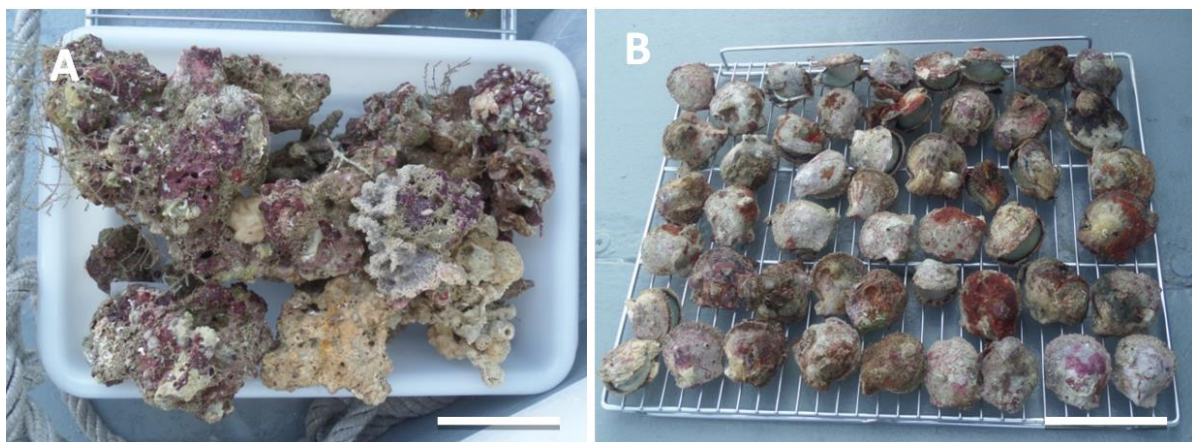


Figure 4.4: A: coral rubble (scale bar= 30cm), B: pearl oysters *Pinctada radiata* (scale bar= 40cm).

Table 4.1: Stations sampled along the East-North coastline of Qatar.

Site	Location	Position	Date	Depth (m)	Seawater temperature (°C)	Salinity (PSU)
1	Station 1	N25 23.000 E52 22.700	5-11-2015	14	30.3	40.2
2	Station 2	N25 24.500 E52 20.000	5-11-2015	16.8	30.2	40.3
3	Station 3	N25 31.000 E52 03.000	6-11-2015	15	30.0	40.3
4	Station 5	N25 45.500 E51 52.000	6-11-2015	22	29.9	39.4
5	Station 7	N25 57.000 E51 54.000	7-11-2015	20	29.8	39.3
6	Station 9	N26 07.000 E51 42.000	7-11-2015	14.2	29.8	39.2

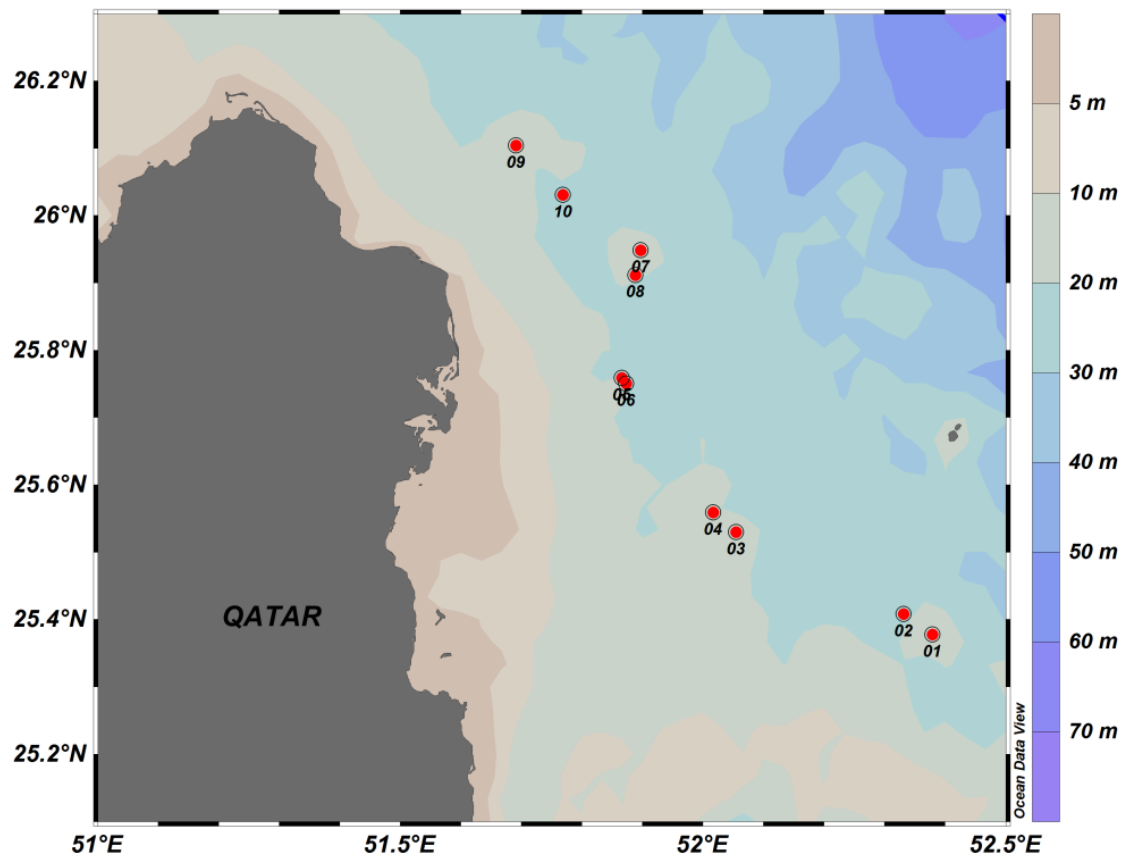


Figure 4.5: Map of stations along the East-North coastline of Qatar.

4.3.2. Material

Bulk coral rubble pieces and shells were rinsed in freshwater and left overnight to dry naturally; this was to remove salt crystals. Bryozoan colonies on dried coral rubble were labelled according to the station; sample number and colony number (e.g. station 1/sample1/colony1). Samples were examined under the microscope for bryozoan species using laboratory facilities on board RV *Janan*. Bryozoan colonies from each station were numbered, drawn and described for identification features and photographed using ZEISS microscope in Environmental Studies Centre at Qatar University. After microscope examination, samples were packed in boxes and sent back to Edinburgh to be further processed at Heriot Watt University.

4.3.3. Scanning electron microscopy for species identification and description

Bryozoa species from Qatar were imaged using LEO 1455 VP SEM electron microscope for the purpose of species description. Prior to scanning the bryozoan colonies were treated with 5 % domestic bleach solution for 1 hour then rinsed with water to remove any organic

materials on the surface of the colonies and ensure that significant identification features were not obscured by contamination. Multiple measurements were taken using Image J of zooid characteristics (zooid length, width, orifice size, avicularia and ovicells) in order to further confirm species identification (Appendix L).

4.3.4. Biodiversity analyses

Diversity indices were calculated from the bryozoan species data spreadsheet to give an understanding of the level of community complexity in each site. Untransformed raw data of number of bryozoan colonies was used to calculate total species (S), total individuals (N), Species richness (d), Pielou's evenness (J), Shannon Wiener diversity ($H[\text{Loge}]$) and Simpson's diversity ($1/\lambda$). Pielou's species evenness is mathematically defined as a diversity index and is a measure of biodiversity which quantifies how equal the community is numerically.

4.3.5. X-ray diffraction analysis (XRD)

Mineralogical analyses were conducted on 9 species of cheilostome Bryozoa at the Mineralogy Department of the Natural History Museum in London (NHM) Figure 4.6.

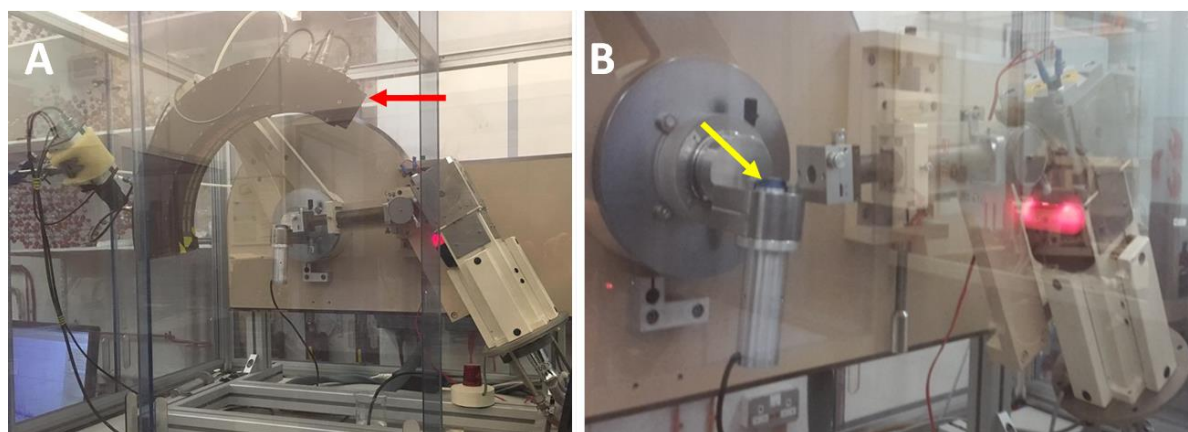


Figure 4.6: Nonius X-ray Diffractometer at the Natural History Museum in London (NHM). A: detector area used to monitor diffracted radiation illustrated by red arrow, B: close-up of sample area illustrated by the yellow arrow.

Bryozoan samples were powdered using a quartz pestle and mortar and affixed using a drop of acetone to single quartz crystal substrates of 3.5mm depth. Quantitative XRD analysis was undertaken to determine the Mol. % MgCO_3 in calcite. X-rays were generated by bombarding a target material, in this case cobalt, with electrons until X-rays were produced; $\text{CoK}\alpha$ radiation has a wavelength (λ) of 1.788965\AA . When the incoming X-rays met the

sample, interference took place between the crystal lattice structure and the X-ray. The X-ray was subsequently diffracted and the angle of diffraction (2θ) and the intensity (counts) were detected and recorded as a spectrum (Figure 4.7, Appendix M). The peak height (measured in counts) of an individual spectra peak, reflects the intensity of the diffracted ray (y-axis) and the position on the x-axis is the angle of diffraction (2θ). In order to calculate Mol. % MgCO_3 in calcite, the midpoint position of the peak (approx. 29.6 on the x-axis), the most intense calcite peak, was measured at 50% of the maximum peak height (Figure 4.8).

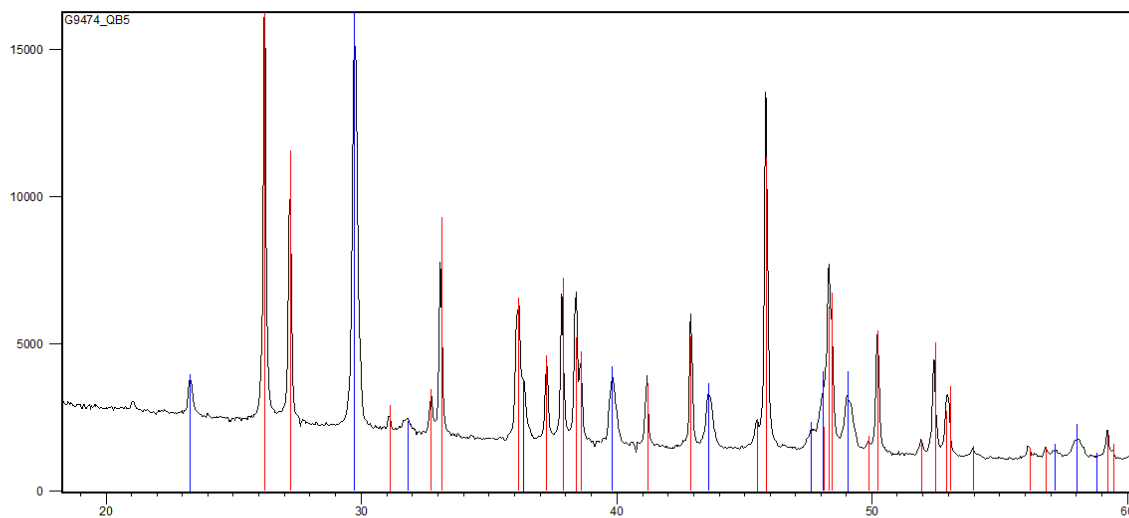


Figure 4.7: XRD spectrum for a bimineralic *Schizoporella errata* bryozoan (red line: aragonite, blue line: intermediate Mg-calcite). Y-axis shows counts of peak intensity. X-axis shows 2θ .

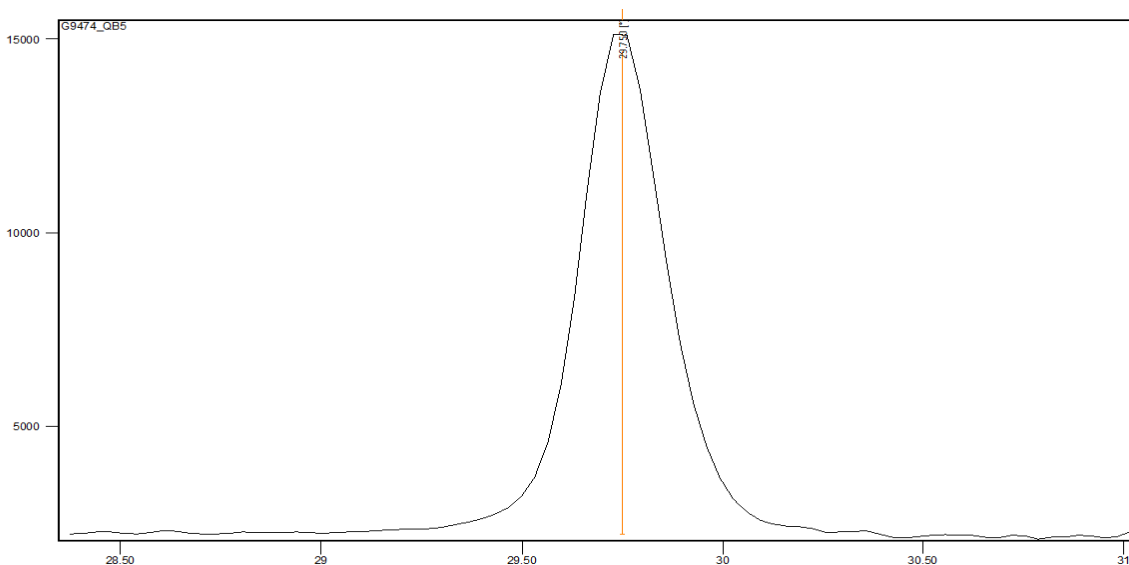


Figure 4.8: Mg-calcite individual peak for a bimineralic *Schizoporella errata* bryozoan (red line: midpoint position of the peak approx. 29.6 on the x-axis). Y-axis shows counts of peak intensity. X-axis shows 2θ .

Using the wavelength of the X-ray radiation (λ) and the 2θ from the spectra, Bragg's Law applied to calculate the d-spacing (d); the spacing between the planes of a crystal lattice.

Equation 1:

$$\text{Bragg's law } 2d \sin \theta = n\lambda$$

By assuming a linear interpolation between the d-spacing of CaCO_3 (3.035\AA) and MgCO_3 (2.742\AA), a calculation of the molecular percent (Mol. %) of MgCO_3 in calcite for the sample can be calculated from the d-spacing (d) of the sample using Equation 2 (Appendix N).

Equation 2:

$$\text{Mol. \% MgCO}_3 \text{ in calcite (sample)} = 3.035 - d(\text{sample}) / 3.035 - 2.742$$

4.4.Results

4.4.1. Qatar habitat description

Bryozoan species were collected from six separate stations along East-North coastline of Qatar. Habitat at each station is described in Table 4.2.

Table 4.2: Stations habitat description.

Location	Habitat description
Station 1	The seabed consisted of cobbles and small boulders in 14m with some slight current. Occasional gorgonians soft corals, rare juvenile oysters, fish burrows and 10% live coral were common in some places. A lost fishing net was seen close to the habitat
Station 2	Medium rippled sand in 16.8m with some slight current. Common juvenile oysters in dense clumps in places often around gorgonians. Marine animals consisted of live coral cover of 2%, some fish and crustaceans. There was drag mark on the seabed, lost rope and cable
Station 3	Remnant oyster bed on coral rock with 40% sediment veneer over patches. Fish burrows and live coral patches 15% and rocky material in rough rows along tidal axis
Station 5	Poorly sorted sediment in thin veneer of a cm or two over coral rock in 22m. Sporadic lumps of coral rubble and conspicuous whip coral gorgonians with occasional hydroid colonies. Common fish burrows and live coral patch 1%
Station 7	Poorly sorted sediment veneer in 20m overlaying large amounts of coral rubble and rock, in places close to the sediment surface, giving rise to dense gorgonian patches and whip corals. Conspicuous cushion stars, fish burrows and upright hydroids. This site had high densities of encrusting bryozoans and foliose calcified bryozoan colonies on the gorgonian bases. Large 50 cm-long undulating cross-tide ripples. Common fish burrows and live coral patch 1%
Station 9	Patches of coral rubble and coral in 14m of water and a slight current interspersed with patches of poorly-sorted sediment veneers under which were more coral rock and rubble. Common fish burrows and 30% live coral in places. Some large coral colonies reported in the area. Lost wire pot was seen close to the habitat

4.4.2. Species description

Species identifications were conducted using ZEISS, light microscope and scanning electron microscopy. Selections of the key species identified are illustrated in Figures 4.9- 4.35.

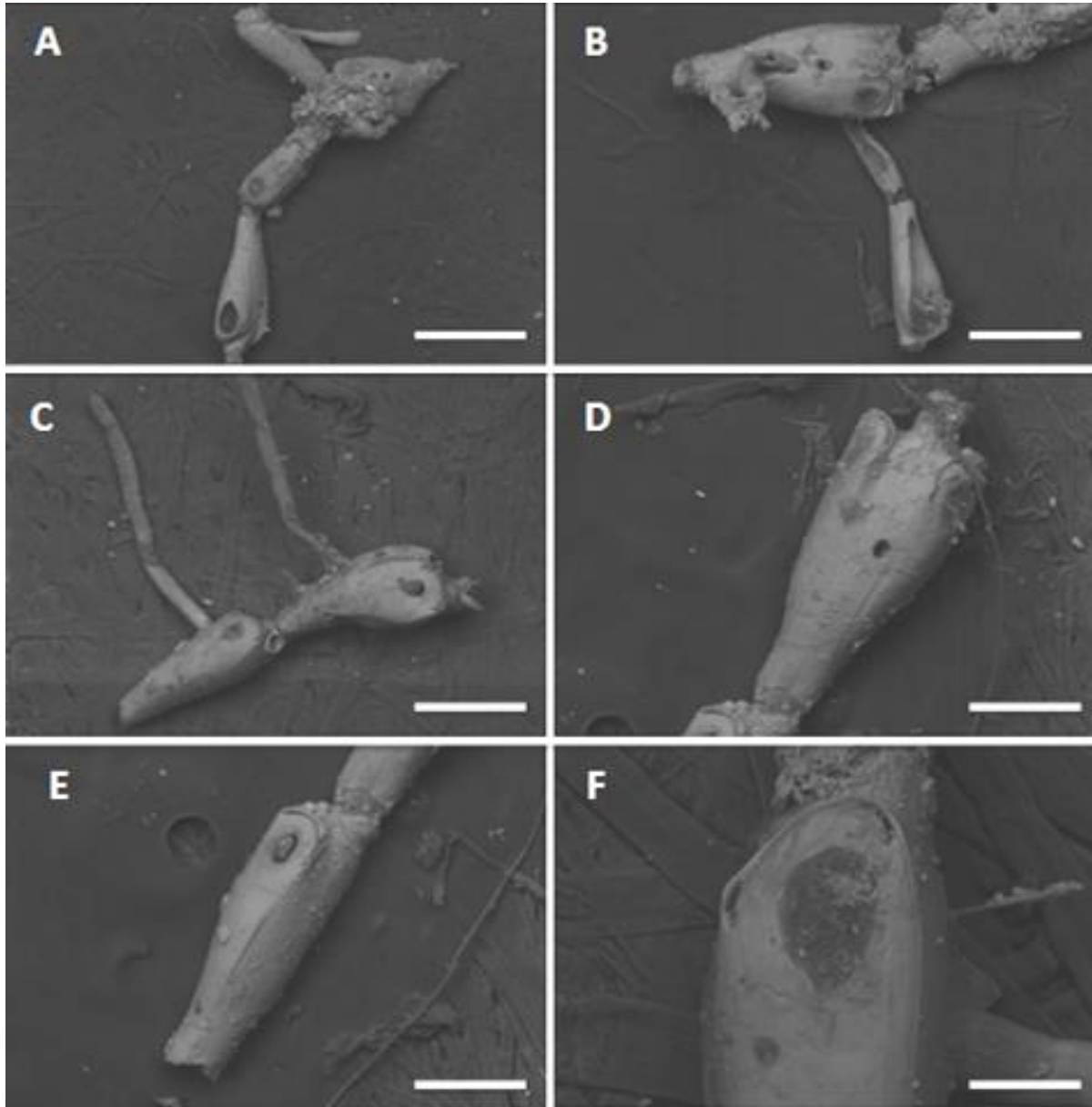


Figure 4.9: Scanning electron micrographs of *Synnotum aegyptiacum*, A: colony overview (scale bar= 200 µm), B: three internodes of paired zooids; proximal older zooid heavily calcified, two holes from rhizoids, young zooid coming off internode towards the bottom of the image; full membranous front (scale bar= 100 µm), C: close-up of side view of two zooids orifice, rhizoids and internode (scale bar= 100 µm), D: close-up of paired zooids and internode (scale bar= 100 µm), E: close-up of side view of zooid orifice and internode (scale bar= 100 µm), F: extra close-up of side view of zooid orifice (scale bar= 20 µm).

Order *Cheilostomatida*

Suborder *Flustrina*

Family *Epistomiidae* Gregory, 1893

Genus *Synnotum* Pieper, 1881

Synnotum aegyptiacum (Audouin, 1826)

Loricaria aegyptiaca – Audouin, 1826: p. 243; Savigny, 1817: Fig. 13, Figs 4¹-5⁴.

Gemellaria avicularis – Pieper, 1881: p. 43, p. 47, Fig. 2, Figs 5-7.

Synnotum aegyptiacum – Harmer, 1926: p. 398, Fig 27, Figs 3, 4; Lagaaij, 1968: p. 351, Fig. 2; Rho & Song, 1980: p.155, Fig. 3, Figs 5, 6; Winston, 1986: p. 57, Figs 19a-g; Tilbrook, Hayward & Gordon, 2001: p. 52, Fig. 6A, C; Liu, Yin & Ma, 2001: p. 500, Fig. 31, Figs 1-3; Tilbrook, 2006: p. 65, pl. 8E-F.

Material

QAT-MGR-00001, collected offshore at 14m depth, found on coral rubble substrata (Appendix J).

Description

Colony erect, autozooids paired, distal portion consisting an internode, frontal area long and narrow, wider distally, becoming gradually narrower proximally to a point, entirely membranous, opercular sclerite completely distal, located in notch on distal wall; zooid walls smooth, with mid-section of autozooids running through preceding internode between membranous areas of autozooids. Avicularia not observed. Rhizoids produced from lateral walls of older zooids; production of rhizoids often associated with closure of frontal areas of autozooids by secondary calcification. One or two circular holes in closure plates distally.

Table 4.3: Characteristics measurements of *Synnotum aegyptiacum* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Paired autozoid length	201.7 \pm 38.3	144.7 – 258.1	7
Paired autozoid width	78.8 \pm 24.1	44.5 – 110.1	7
Orifice length	102.9 \pm 54.9	52.7 – 187.6	7
Orifice width	54.4 \pm 20.4	36.7 – 95.4	7
Internode length	47.4 \pm 7.1	39.1 – 57.3	6
Internode width	106.3 \pm 34.3	64.2 – 147.9	6
Hole length	38.5 \pm 18.3	22.9 – 69.8	7
Hole width	35 \pm 14.4	20.5 – 56.6	7

Remarks

Synnotum aegyptiacum is characterised by its erect colony form of slender jointed bifurcating branches. In Qatar this species was found only in station 1 encrusting coral rubble. *Synnotum aegyptiacum* has been recorded in warm temperate and tropical waters at depth to 82m (Tilbrook, 2006). This species was found in the Solomon Islands (Tilbrook, 2006) and the Mediterranean Sea (Gerovasileiou and Rosso, 2016). There are no previous records of this species in the Arabian Gulf.

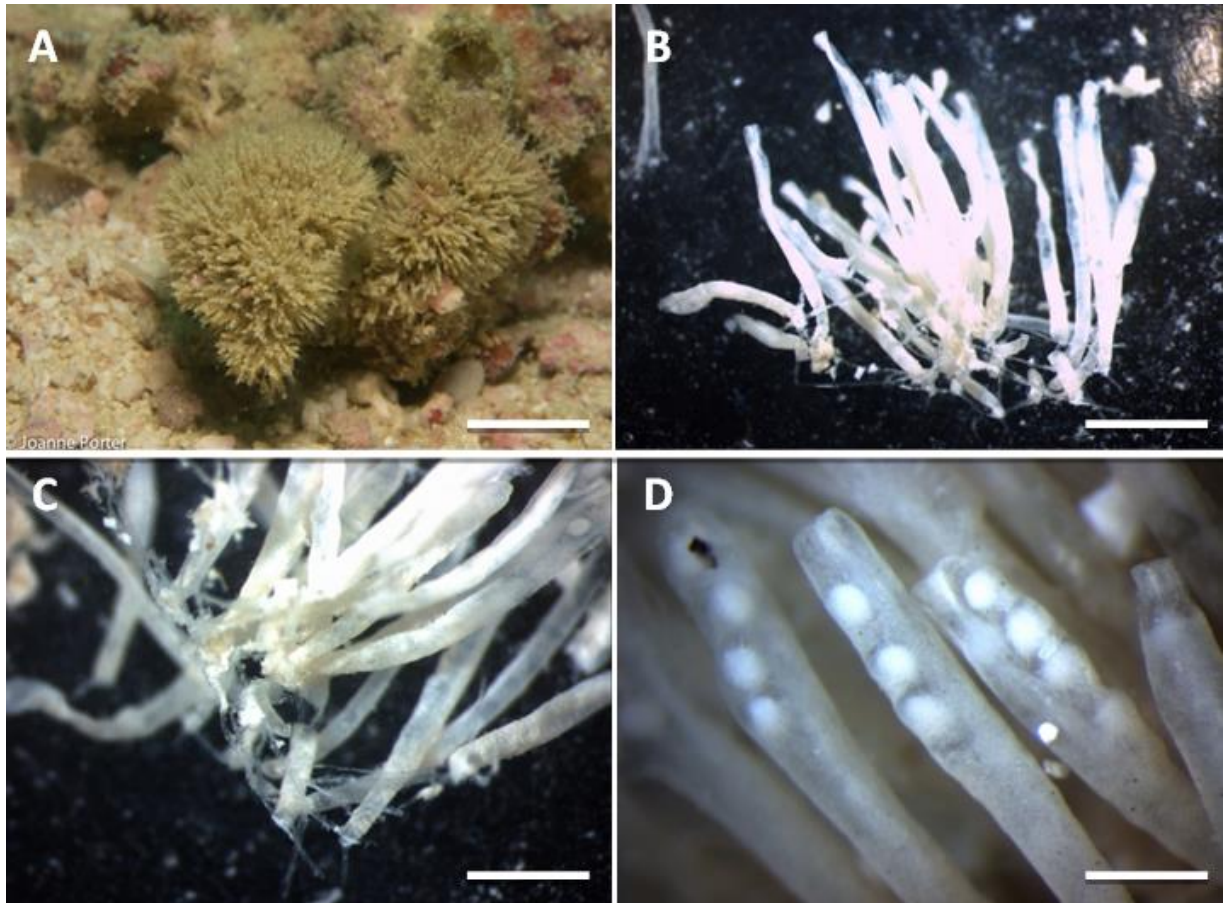


Figure 4.10: A: *Nolella* sp. growing on coral rubble substrata (scale bar= 3 cm), B: overview of zooids connected by basal stolon (scale bar= 20 mm), C: close-up of stolon (scale bar= 10 mm), D: extra close-up of zooids with embryos, up to 4 embryos were observed in a zooid (scale bar= 4 mm).

Order *Ctenostomatida*

Suborder *Victorellina*

Superfamily *Victorelloidea* Hincks, 1880

Family *Nolellidae* Harmer, 1915

Genus *Nolella* Gosse, 1855

Nolella sp.

Material

Qatar: QTR-MGR-00002, collected offshore at 22m depth, found on coral rubble substrata (Appendix J).

Description

Colony comprising narrow tubular zooids, usually connected by basal stolon form elongations, very narrow relative to zooid size. Individual zooids are cylindrical, white to tan in colour. Orifice flat at top of zooid tube, often square in outline. Three to four pale yellow embryos brooded in zooids, upper portions of which may then become slightly dilated.

Table 4.4: Characteristics measurements of *Nolella* sp. species found in Qatar.

Measurements	Mean \pm SD (mm)	Range (mm)	Zooids Number
Autozooid length	0.44 ± 0.09	0.29 – 0.56	10
Autozooid width	0.03 ± 0.005	0.027 – 0.045	10
Orifice length	0.027 ± 0.004	0.021 – 0.035	10
Stolon width	0.013 ± 0.002	0.01 – 0.017	5
Embryos length	0.026 ± 0.004	0.021 – 0.035	10
Embryos width	0.02 ± 0.003	0.015 – 0.026	10

Remarks

The tubes of the zooids resemble tubes of polychaetes or amphipods, and often go unrecognized unless tentacle crowns are expanded, but the squared-off orifice shape helps distinguish the tubes as belonging to *Nolella*. *Nolella* species from Qatar did not match the species in d'Hondt (1983) keys for the identification of Ctenostomatous Bryozoa. *Nolella* species from Qatar differs from *Nolella sawayai* from Brazil described by Marcus (1938) in the absence of spines. *Nolella* species from Qatar also differs from *Nolella stipata* from Brazil described by Vieira et al. (2014) in zooid size; being the latter measuring 1.535–3.186 mm in length and 0.133–0.247 mm in width. In Qatar one colony in station 5 and 4 colonies in station 7 of *Nolella* sp. species were attached to stems of hydroids, and found on sea fan, and shells.

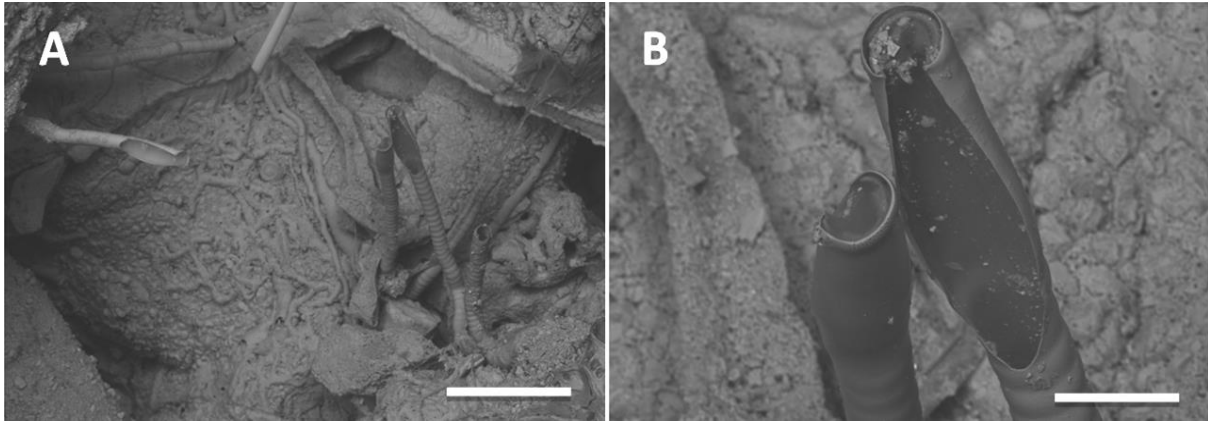


Figure 4.11: Scanning electron micrographs of *Aetea ligulata*, A: zooids overview (scale bar=200 µm), B: close-up of zooids frontal membrane (scale bar=20 µm).

Suborder *Inovicellina*

Family *Aeteidae* Smitt, 1868

Genus *Aetea* Lamouroux, 1812

Aetea ligulata Busk, 1852

Aetea ligulata – Prenant & Bobin, 1966: p. 89, Fig. 21, IV, VI (cum syn.); Gordon, 1984: p. 39, pl. 8, Figs E, F; Tilbrook, Hayward & Gordon, 2001: p. 37, Fig. 2A.

Aetea ligulata – Busk, 1852: p. 31, pl. 42.

Material

Qatar: QTR-MGR-00003, collected offshore at 14m depth, found on coral rubble substrata (Appendix J).

Description

Colony white, ramifying and moniliform, with a zooid stem arising from each dilation. Stems generally tall and slender, distal portion, bearing the frontal membrane, scarcely wider than the stem, occupying about one-third of the free length; the stem is characterized by its broad, rounded, horizontal corrugations.

Table 4.5: Characteristics measurements of *Aetea ligulata* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Stem length	655 ± 280.3	456.7 – 853.28	2
Stem width	54.2 ± 2.1	52.7 – 55.7	2
Frontal membrane length	201 ± 64.8	126.2 – 241.9	3
Frontal membrane width	69.9 ± 11.7	62.2 – 83.4	3

Remarks

This species has been originally described from the Atlantic, and has been recorded from warm temperate and tropical seas worldwide. This species was found in the southern South America, Brazil, and West Africa (Tilbrook et al., 2001). In Qatar three colonies of this species were found in station 1 and 9 encrusting coral rubble.

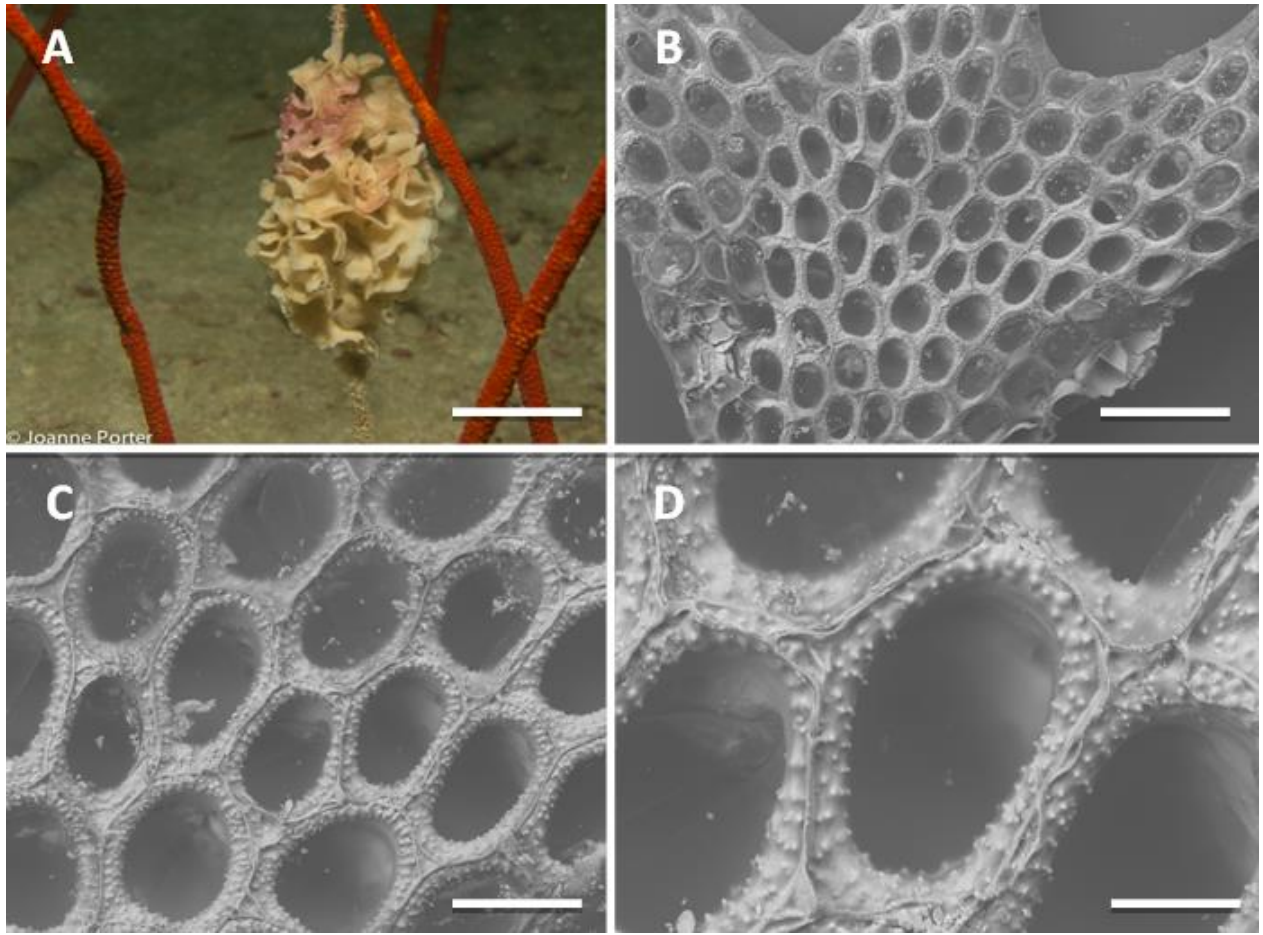


Figure 4.12: A: *Biflustra* sp. attached to a gorgonian soft coral (scale bar=3.5 cm), B: Scanning electron micrograph of *Biflustra* sp. (scale bar=100 μ m), C: close-up of a group of zooids (scale bar=100 μ m), D: extra close-up of zooids frontal membrane (scale bar=20 μ m).

Suborder *Malacostegina*

Family *Membraniporidae* Busk, 1852

Genus *Biflustra* d'Orbigny, 1852

Biflustra sp.

Material

Qatar: QTR-MGR-00004, collected offshore at 20 m depth, found attached to gorgonian soft coral substrata (Appendix J).

Description

Colony grows as encrusting or erect, white to tan in colour. Autozooids are irregularly polygonal or rectangular, separated by raised lateral walls. The gymnocyst are absent. The cryptocyst calcification is granular, occupying one quarter to one third of frontal area, surrounding oval opesia. Spines, avicularia, and ovicells are not observed.

Table 4.6: Characteristics measurements of *Biflustra* sp. species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	199.9 \pm 27.1	149.2 – 246.5	30
Autozoid width	138.4 \pm 19.3	107.7 – 177.7	30
Frontal membrane length	141.1 \pm 13.4	116.8 – 179.3	30
Frontal membrane width	93.6 \pm 14. 7	73.3 – 135.3	30

Remarks

Biflustra sp. from Qatar is characterised by the simple appearance of the autozooids. It differs from *Biflustra arborescens* (Canu and Bassler, 1928) by the absence of spines and also differs from *Biflustra perfragilis* (MacGillivray, 1881) found in Bass Strait, Victoria and Tasmania by the absence of avicularia. In Qatar three colonies of this species were found attached to a gorgonian soft coral (sea whip) in station 7 as shown in Figure 4.12A.

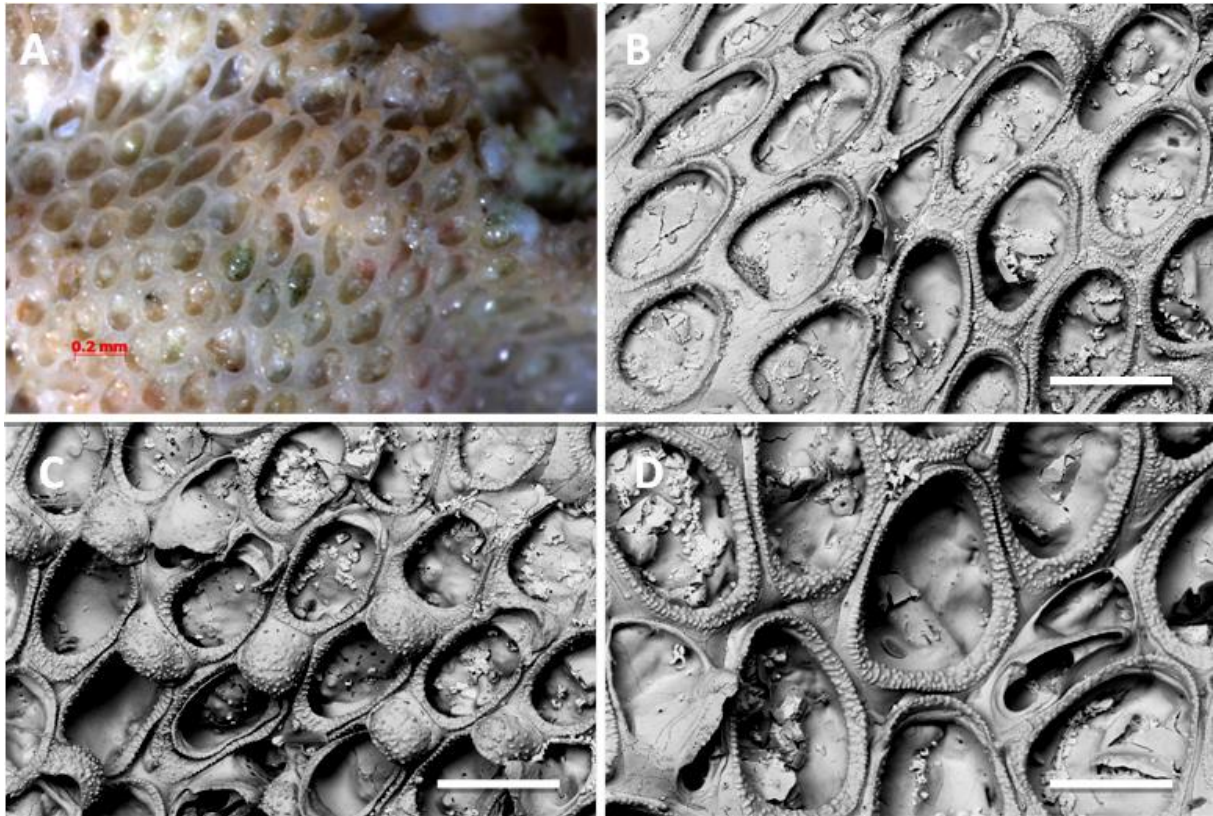


Figure 4.13: A: ZEISS microscope picture of *Parellisina* sp. (scale bar= 0.2 mm), B: scanning electron micrograph of *Parellisina* sp. (scale bar= 200 µm), C: close-up of an ovicellate group of zooids (scale bar= 200 µm), D: extra close-up of zooids frontal membrane and avicularium (scale bar= 100 µm).

Family *Calloporidae* Norman, 1903

Genus *Parellisina*, Harmer, 1926

Parellisina sp.

Material

Qatar: QTR-MGR-00005, collected offshore at 14m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as a lightly calcified, thin, and spreading sheet. Autozooids are irregularly oval, separated by deep grooves, the gymnocyst is scarcely visible and it is reduced to a minimal area of smooth calcification at the proximal end of the autozooid. The cryptocyst is narrow, finely granular with a sloping rim bordering the opesia. There are no spines present. Interzooidal avicularia are irregularly disposed, usually frequent, and the cystid is largely

obscured. The rostrum is slightly acute to the frontal plane, it is straight to moderately curved, directed distally, with a semicircular opesia proximal to the condyles and a narrow, almost parallel-sided distal portion supporting the slender, acuminate mandible. Ovicells are hemispherical, slightly immersed; ectooecium largely membranous frontally, entooecium granular.

Table 4.7: Characteristics measurements of *Parellisina* sp. species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	319.1 \pm 50.69	242.5 – 434.7	30
Autozoid width	176.8 \pm 19.4	133.3 – 209.2	30
Frontal membrane length	238.8 \pm 35.3	185.5 – 321.1	30
Frontal membrane width	142.2 \pm 23.9	114.6 – 250.9	30
Ovicell length	147.4 \pm 54.5	76.7 – 238.6	13
Ovicell width	183.1 \pm 72.7	75.9 – 281.4	13
Avicularium length	175.6 \pm 17.6	147 – 189.1	5
Avicularium width	60.6 \pm 3.3	56.9 – 64.7	5

Remarks

Species of *Parellisina* species are differentiated by the shape of the curved rostrum of the avicularium (Tilbrook, 2006). The *Parellisina* species from Qatar differs from *Parellisina mboliensis* from the Solomon Islands described by Tilbrook (2006) where *Parellisina mboliensis* is characterised by the presence of spines and the vicarious avicularia with semicircular rostrum that is larger than its associated vestigial kenozooid, compared to the Qatar species which does not have these characters.

In Qatar *Parellisina* species was found encrusting on coral rubble substrata. Four colonies were recorded along the coastline of Qatar; two colonies in station 1, one colony in station 5 and one colony in station 9.

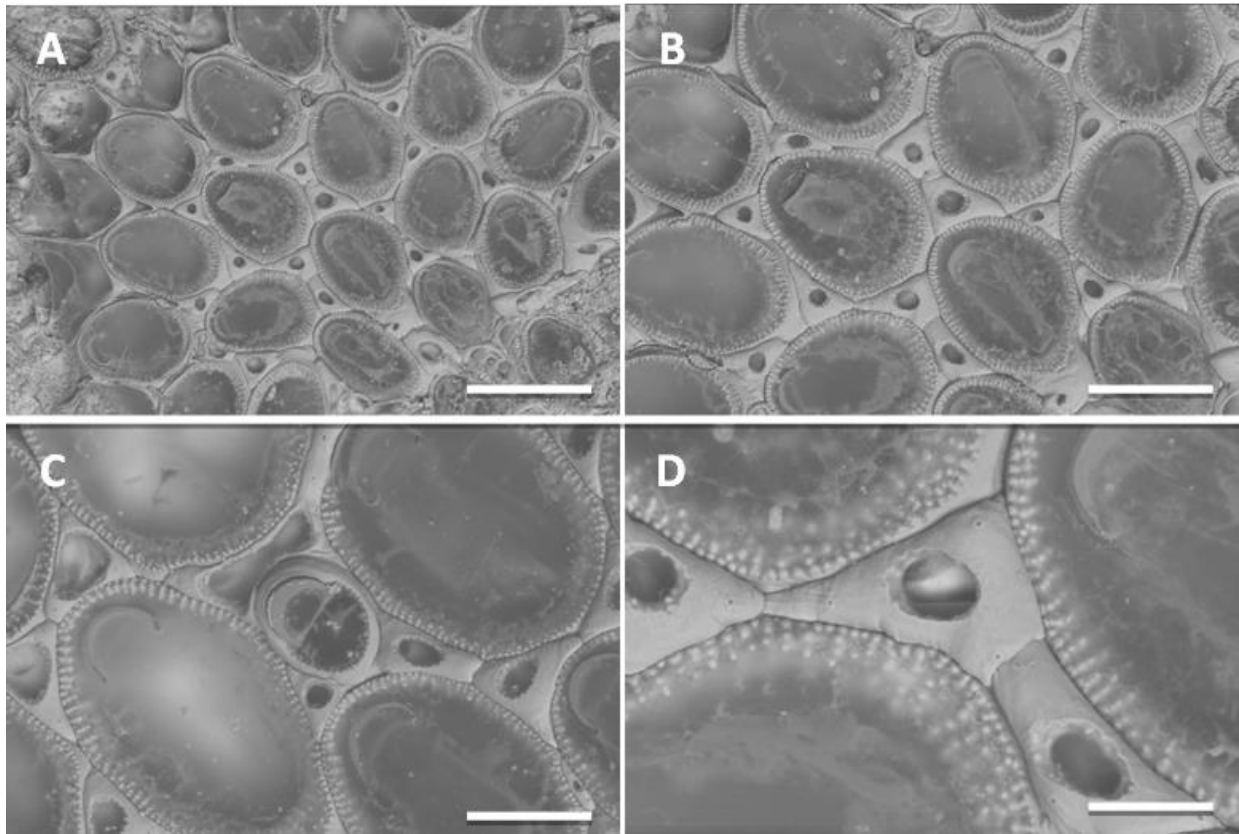


Figure 4.14: Scanning electron micrographs of *Akatopora* sp., A: close-up of a group of zooids (scale bar= 200 µm), B: close-up of zooids frontal membrane and kenozooids (scale bar= 100 µm), C: close-up avicularium (scale bar= 20 µm), D: extra close-up of kenozooids (scale bar= 10 µm).

Family *Akatoporidae* Vigneaux, 1949

Genus *Akatopora* Davis, 1934

Akatopora sp.

Material

Qatar: QTR-MGR-00006, collected offshore at 16.8m depth, found on sand dollar substrata (Appendix J).

Description

The colony grows as a pale pink unilaminar, spreading sheet. Autozooids are oval to elliptical, trigonal in places. The opesia are oval, lacking gymnocyst, the cryptocyst is distinct, relatively broad, and granular. Zooidal boundaries are distinct, separated by fine grooves. Avicularia are slightly elevated and bear a semicircular mandible. Interzooidal

triangular to oval in outline kenozooids occur around each autozoid. The autozoid has a membranous frontal surface underlain by granular cryptocyst.

Table 4.8: Characteristics measurements of *Akatopora* sp. species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	427.4 \pm 41	365 – 523.4	12
Autozoid width	314.5 \pm 36.9	240.7 – 381	12
Frontal membrane length	344.8 \pm 28.4	292.9 – 402	12
Frontal membrane width	229.6 \pm 35.6	168.2 – 286.2	12
Avicularium length	471.2 \pm 0	471.2 – 471.2	1
Avicularium width	358.5 \pm 0	358.5 – 358.5	1
Kenozooids length	155.3 \pm 39.1	102.7 – 234.7	15
Kenozooids width	75.1 \pm 22.3	25.2 – 115.1	15

Remarks

The distinctive kenozooids are a typical characteristic feature for the genus *Akatopora*. The *Akatopora* species from Qatar differs from *Akatopora tincta* (Hastings, 1930) from the Pacific in zooid size; the latter measuring 114.9–157.2 μm in length and 74.7–120.5 μm in width. The shape of the avicularia of Qatar species differs from the fossil specimen of *Akatopora* from Gujarat, India described by Guha and Gopikrishna (2005) in which the latter avicularia is similar in shape to kenozooids. Guha and Gopikrishna (2005) described the ovicells of *Akatopora aidaensis* as small, endozooecial, cap-like in appearance and very rare (no image, just a description in the text). Ovicells were not observed in material from Qatar. Four colonies of *Akatopora* sp. were found in Qatar, three colonies in station 2, and one colony in station 5.

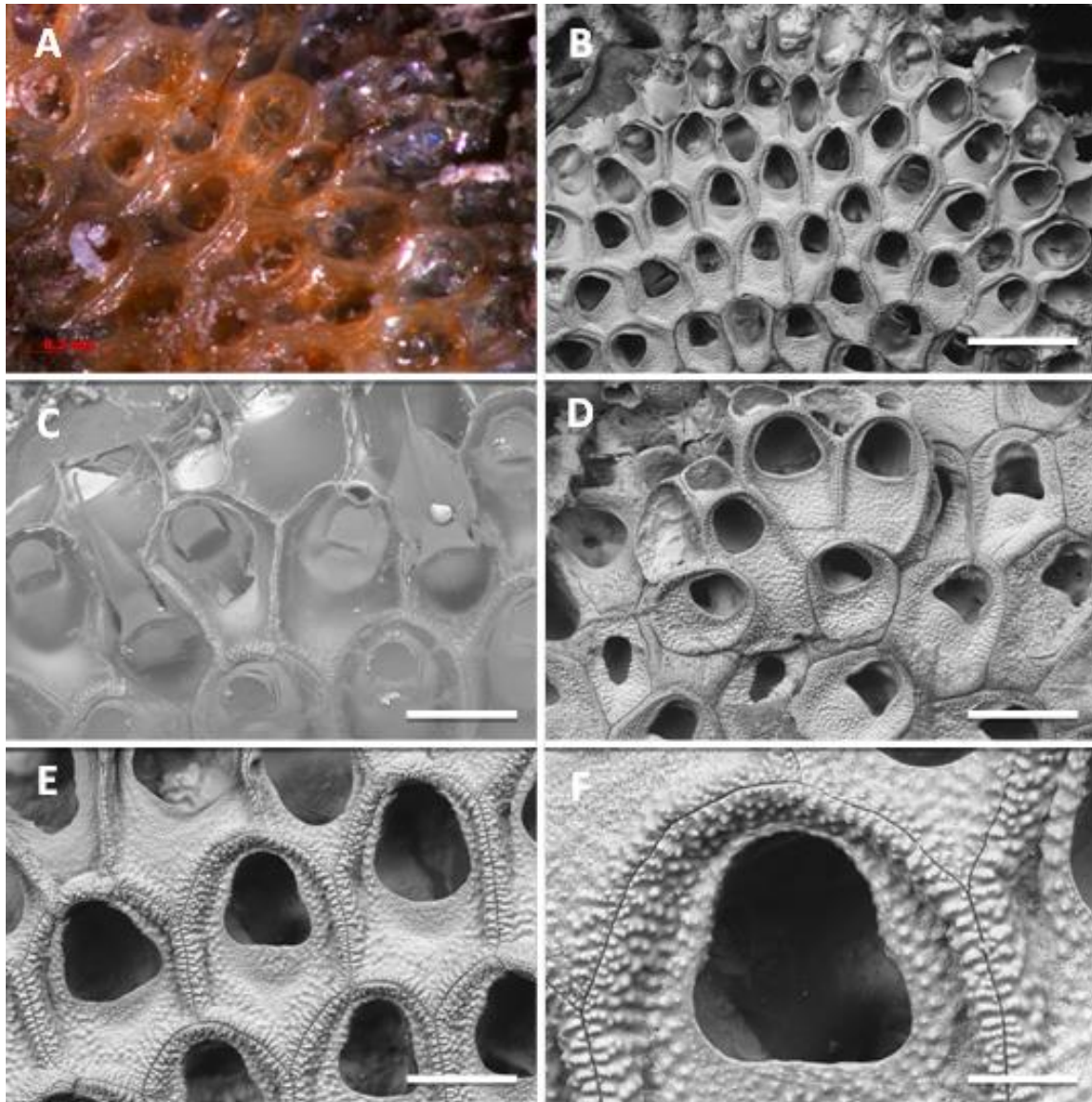


Figure 4.15: A: ZEISS microscope picture of *Smittipora harmeriana* (scale bar=0.2mm), B: scanning electron micrograph of *Smittipora harmeriana* (scale bar= 200 μ m), C: close-up of colony edge before bleaching showing avicularium mandible hooked tip (scale bar= 100 μ m), D: close-up of a group of zooid frontal membrane and avicularium (scale bar= 100 μ m), E: close-up of three zooids (scale bar= 100 μ m), F: extra close-up of zooids frontal membrane (scale bar= 20 μ m).

Family *Onychocellidae* Jullien, 1882

Genus *Smittipora* Jullien, 1882

Smittipora harmeriana (Canu & Bassler, 1929)

Smittipora abyssicola – MacGillivray, 1891: p. 80, Fig. 9, Fig. 4; Harmer, 1926: p. 259, Fig. 16, Figs, 10-13.

Velumella harmeriana – Canu & Bassler, 1929: p. 128.

Smittipora harmeriana – Winston, 1986: p.10; Winston & Heimberg, 1986: p. 11, Figs. 23, 24, Hayward, 1988: p. 281, Fig. 1, fig. C; Tilbrook, 2006: p.76, pl.12B.

Material

Qatar: QTR-MGR-00007, collected offshore at 14 m depth, found attached to coral rubble substrata (Appendix J).

Description:

The colony grows as a unilaminar crust. Autozooids are hexagonal to irregularly polygonal, concave and are separated by a thick raised marginal rim. The membranous frontal membrane is translucent and light orange. It covers a coarsely granular cryptocystal frontal surface. The opesia are large, slightly longer than wide and bell-shaped in distal half of zooid. The opesia are surrounded by frontal cryptocystal, distal border rounded with wide ledge pointing proximally, proximal edge smooth, slightly convex, lip arching frontally a little and dipping slightly at each lateral corner. Operculum light orange-brown in colour and is smaller than the opesia. The avicularia are shorter than the autozooids and are narrow. The cryptocystal is coarsely granular and concave. The opesia are oval, only slightly wider distally and centrally located. The proximal border is denticulate but smooth distally. A pair of condyles are developed approximately two-thirds the way along each lateral wall. The distal end of the avicularium is rounded, the mandible is short and the rachis is orange-brown in colour, hooked at the tip. Its translucent light-orange blades reach approximately 80% of the length of the rachis (Tilbrook, 2006).

Table 4.9: Characteristics measurements of *Smittipora harmeriana* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozooid length	293.1 \pm 40.1	220.8 – 353.5	22
Autozooid width	215.9 \pm 24.8	157.2 – 257.1	22
Frontal membrane length	129 \pm 15.6	91.2 – 163	22
Frontal membrane width	105.5 \pm 12	81 – 126	22
Avicularium length	382 \pm 74.6	298.1 – 447.1	4
Avicularium width	194 \pm 45.5	151.3 – 236.1	4

Remarks:

Tilbrook (2006) described two species of *Smittipora* from the Solomon Islands. *Smittipora harmeriana* is characterised by the shape of the opesia and avicularium. *Smittipora harmeriana* differs from *Smittipora cordiformis* in having large opesia and its avicularia do not curve which is a diagnostic character of *Smittipora cordiformis* (Tilbrook, 2006). The material from Qatar matches the description of *Smittipora harmeriana* because of the shape of the opesia and avicularia. Only one colony of this species was found in Qatar encrusting coral rubble in station 1. *Smittipora harmeriana* has been recorded from Torres Strait, Indonesia and westwards into the Indian Ocean, from north Western Australia to Mauritius and the Mascarene Islands (Tilbrook, 2006).

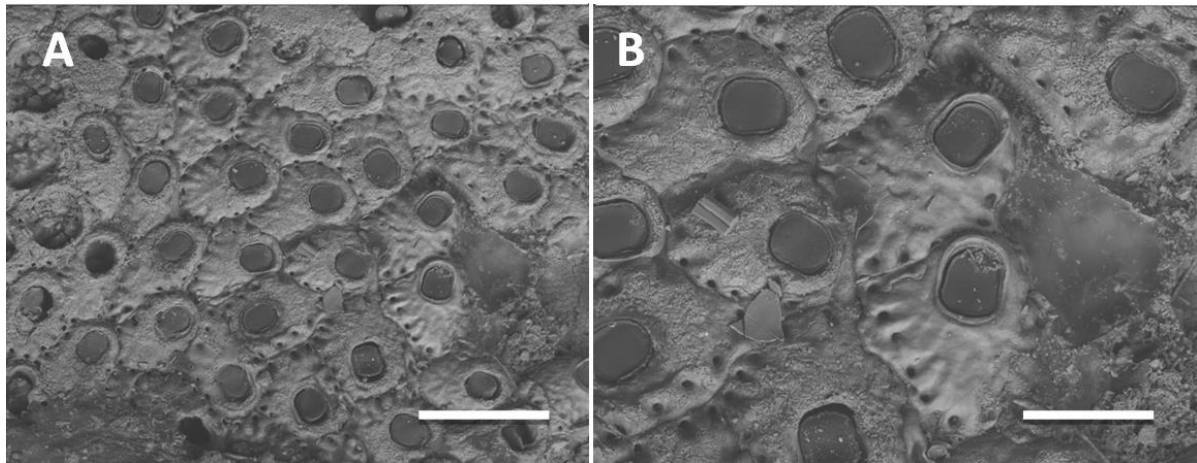


Figure 4.16: A, B: Scanning electron micrographs of *Odontoporella* sp. (scale bar= 200 μ m).

Family *Hippoporidridae* Vigneaux, 1949

Genus *Odontoporella* H  jjas, 1894

Odontoporella sp.

Material

Qatar: QTR-MGR-00008, collected offshore at 22 m depth, found attached to pearl oyster shell *Pinctada radiata* substrata (Appendix J).

Description:

The colony grows as an encrusting sheet, white in colour, unilaminar to multilaminar growing on a shell substratum. The autozooids are clearly separated by deep grooves. The frontal shield is convex and smooth with six to eight large pores around the margin. The orifice is bell-shaped with the broad poster generally almost as wide as the anter. There are well-developed condyles at the point where the orifice is constricted. No oral spines were observed. No avicularia were present. The ancestrula zooid was not seen in this material.

Table 4.10: Characteristics measurements of *Odontoporella* sp. species found in Qatar.

Measurements	Mean \pm SD (μ m)	Range (μ m)	Zooids Number
Autozooid length	282.3 \pm 30.6	237.2 – 371.3	30
Autozooid width	188.3 \pm 31	117 – 244.5	30
Orifice length	97 \pm 8.8	78.8 – 116.8	30
Orifice width	77.7 \pm 6.3	66.4 – 90.4	30

Remarks

The *Odontoporella* species from Qatar differs from *Odontoporella adpressa* and *Odontoporella bishopi* from New Zealand described by Carter and Gordon (2007) in which *Odontoporella adpressa* is characterised by a granular frontal shield with 12–16 radial ridges and *Odontoporella bishopi* is characterised by the presence of an avicularia. The species from Qatar did not have the radial ridges and the number of pores differed, therefore this is likely to be a separate species

Three colonies of the Qatar species were found, these were associated with various shells, two colonies were recorded from station 1 found on a gastropod shell and one colony was recorded from station 5 found on a pearl oyster shell *Pinctada radiata*.

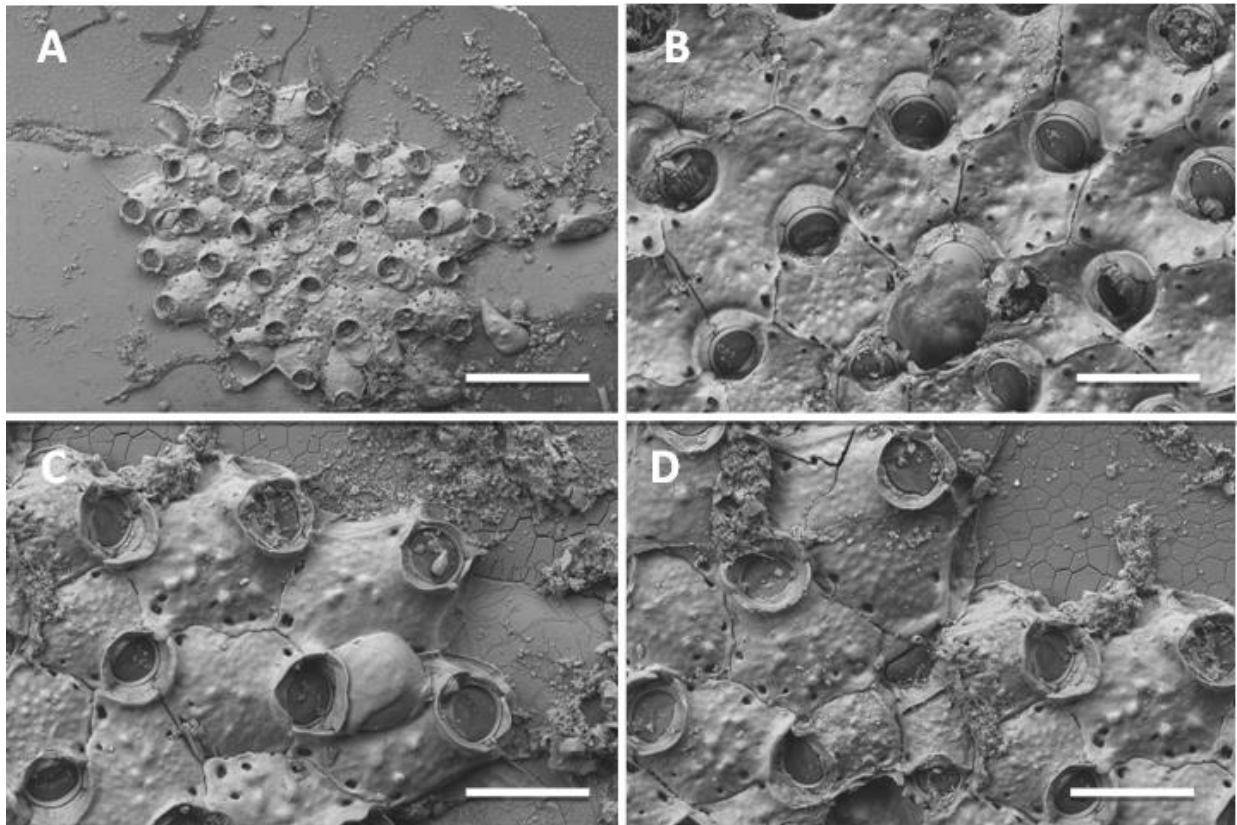


Figure 4.17: Scanning electron micrographs of *Predanophora longiuscula*. A; colony overview (scale bar= 100 μm). B; close-up of a group of zooids scale bar= 100 μm), C: close-up of zooids orifice and ovicell (scale bar= 100 μm), D: close-up of ancestrula zooid (scale bar= 100 μm).

Family *Celleporidae* Johnston, 1838

Genus *Predanophora* Tilbrook, 2006

Predanophora longiuscula (Harmer, 1957)

Rhynchozoon corrugatum – Waters, 1909: p. 158, pl. 12, Figs. 14-16.

Drepanophora longiuscula – Harmer 1957: p. 1081, Fig 63A-C.

Drepanophora longiuscula – Dumont, 1981: p. 636.

Predanophora longiuscula – Tilbrook, 2006: p.283, pl. 63A-C.

Material

Qatar: QTR-MGR-00009, collected offshore at 14.2m depth, found on pear oyster shell *Pinctada radiata* substrata (Appendix J).

Description

The colony grows as a unilaminar encrusting sheet. The autozooids are small, oval to hexagonal, and are distinct, separated by shallow grooves. The frontal shield is convex and smooth with six small pores around the margin. The primary orifice is sub-orbicular, it is wider than long, with the anter large and round. The peristome is flared and bears a small, oval, suboral avicularium. The ovicell is longer than wide. There are paired, lozenge-shaped longitudinal foramina, reaching almost the entire length of the ovicell. The ovicell is not closed by the maternal operculum, it open into the peristome above the primary orifice (Tilbrook, 2006). The peristome is in close proximity to the proximal rim of the ovicell. The ancestrula is seen here, surrounded by five spines.

Table 4.11: Characteristics measurements of *Predanophora longiuscula* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	190.3 \pm 26.7	141.7 – 239.7	28
Autozoid width	153.6 \pm 39.4	80.7 – 271	28
Orifice length	49.4 \pm 9.1	30.8 – 66.5	26
Orifice width	53 \pm 6.6	42.2 – 67.6	26
Ovicell length	74.3 \pm 9	64.9 – 83.1	4
Ovicell width	91.2 \pm 17.4	67.4 – 106.2	4
Ansestrula length	205.8 \pm 0	205.8 – 205.8	1
Ansestrula width	163.2 \pm 0	163.2 – 163.2	1

Remarks:

Predanophora longiuscula is characterised by its, tuberculate frontal shield, its flared peristome with associated suboral avicularium and by the paired lozenge-shaped foramina through the ectooecium. The primary orifice initially sits within a raised rim that is superseded by the flared peristome. The peristome is developed from the cystid producing the oral avicularium and originating from one of the two distolateral pores. The ovicell formed from the distal edge of the oral area of its maternal zooid. Then it rests on the frontal shield of the distal autozoid producing the distal part of the peristome (Tilbrook, 2006).

In Qatar only one single colony of this species was found on a pearl oyster shell *Pinctada radiata* from Station 9.

Predanophora longiuscula was originally described Thorneley's (1905) *Rhyncopora corrugata* by Waters (1909) from the Bay of Suez, *Predanophora longiuscula* has not been found since Tilbrook (2006). Only a single specimen exists of this distinct species. A poor preserved specimen from Sri Lanka (NHM unregistered, ex 1936. 12.30.60B), and now this is the second specimen of this species, and the first record from Qatar.

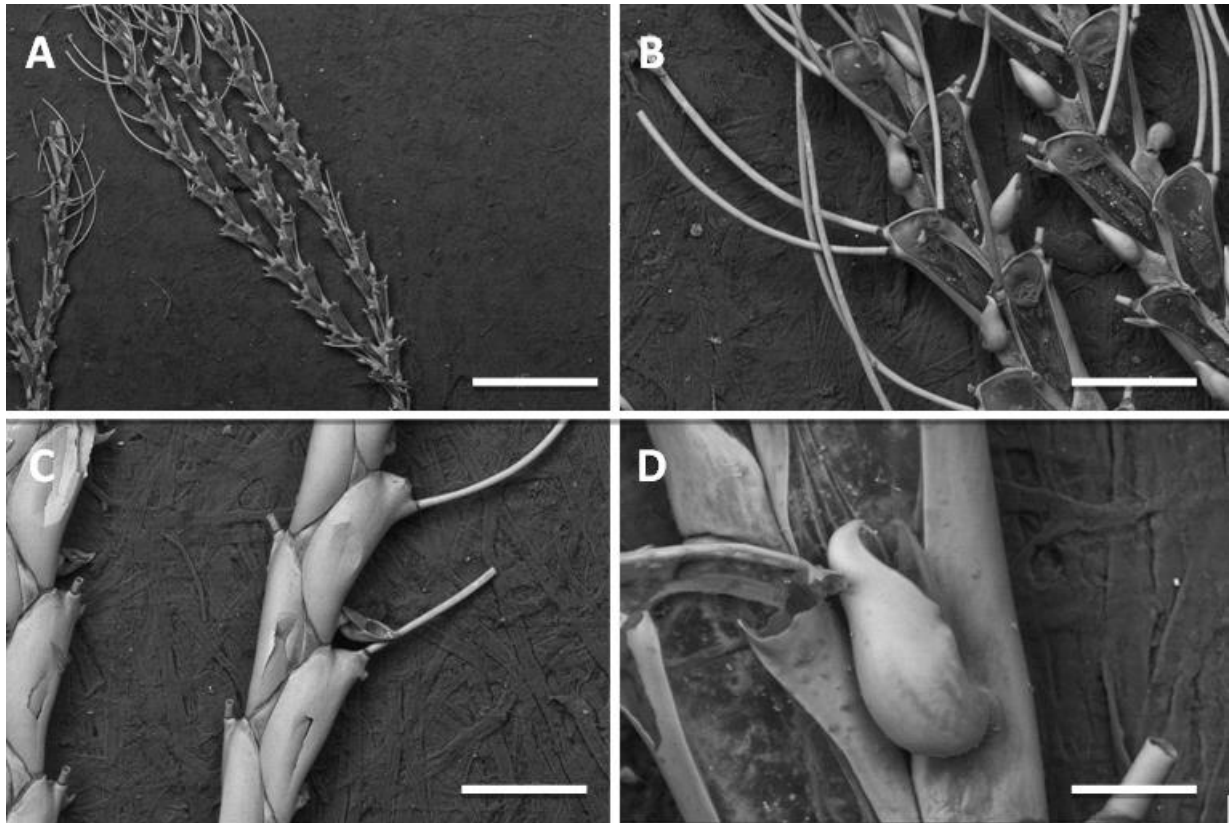


Figure 4.18: Scanning electron micrographs of *Caulibugula* sp., A: overview of biserial branches (scale bar= 200 µm), B: close-up of zooids frontal membrane, spines and avicularium (scale bar= 100 µm), C: close-up of the back of the zooid and an open avicularium mandible (scale bar= 100 µm), D: extra close-up of avicularium showing the long beak-like hooked rostrum (scale bar= 20 µm).

Family *Bugulidae* Gray, 1848

Genus *Caulibugula* Verrill, 1900

Caulibugula sp.

Material

Qatar: QTR-MGR-00010, collected offshore at 14 m depth, found growing on coral rubble substrata (Appendix J).

Description

The colony is erect, growing from a system of stolon-like cylindrical kenozooids, yellowish-brown in colour. The autozooids fan out; the colony is quite robust and is arranged in biserial branches from a single proximal zooid, rectangular or narrowing below, almost the entire frontal surface is membranous. Spines are common, very long, curved with formula 2:1. The avicularia is large attached to the lower third of the outer side of the lateral wall, with long, bulbous head and long beak-like hooked rostrum, mandible long, with hooked tip. Ovicells not present.

Table 4.12: Characteristics measurements of *Caulibugula* sp. species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozooid length	70.9 \pm 6.7	60.5 – 89.5	30
Autozooid width	18.8 \pm 1.9	15.3 – 23.6	30
Frontal membrane length	54.7 \pm 4.4	48.6 – 67.3	30
Frontal membrane width	14.1 \pm 2.3	7.3 – 18.1	30
Avicularium length	21.5 \pm 1.9	18.1 – 15.9	29
Avicularium width	7.8 \pm 0.9	6.4 – 9.6	29
Spines length	138.3 \pm 33.2	99.6 – 180.9	8

Remarks:

Harmer (1926) discussed the diagnostic characters to differentiate *Caulibugula* species which are the numbers and lengths of distal spines, the position and shape of the avicularia, and the overall shape of the autozooids, in particular their opesia (Tilbrook, 2006). *Caulibugula* sp. from Qatar has 3 spines and differs from *Caulibugula exilis* from the Indo-pacific that has six to eight long joined spines and also differs from *Caulibugula lunga* from the Solomon Islands where spines numbers change in the fan (Tilbrook, 2006). The characters of the material from Qatar do not match the species described by Harmer (1926) and Tilbrook (2006) therefore the Qatar material is likely to be a new species. In the coastal waters of Qatar only one colony of this species was found in Station 1 growing on coral rubble.

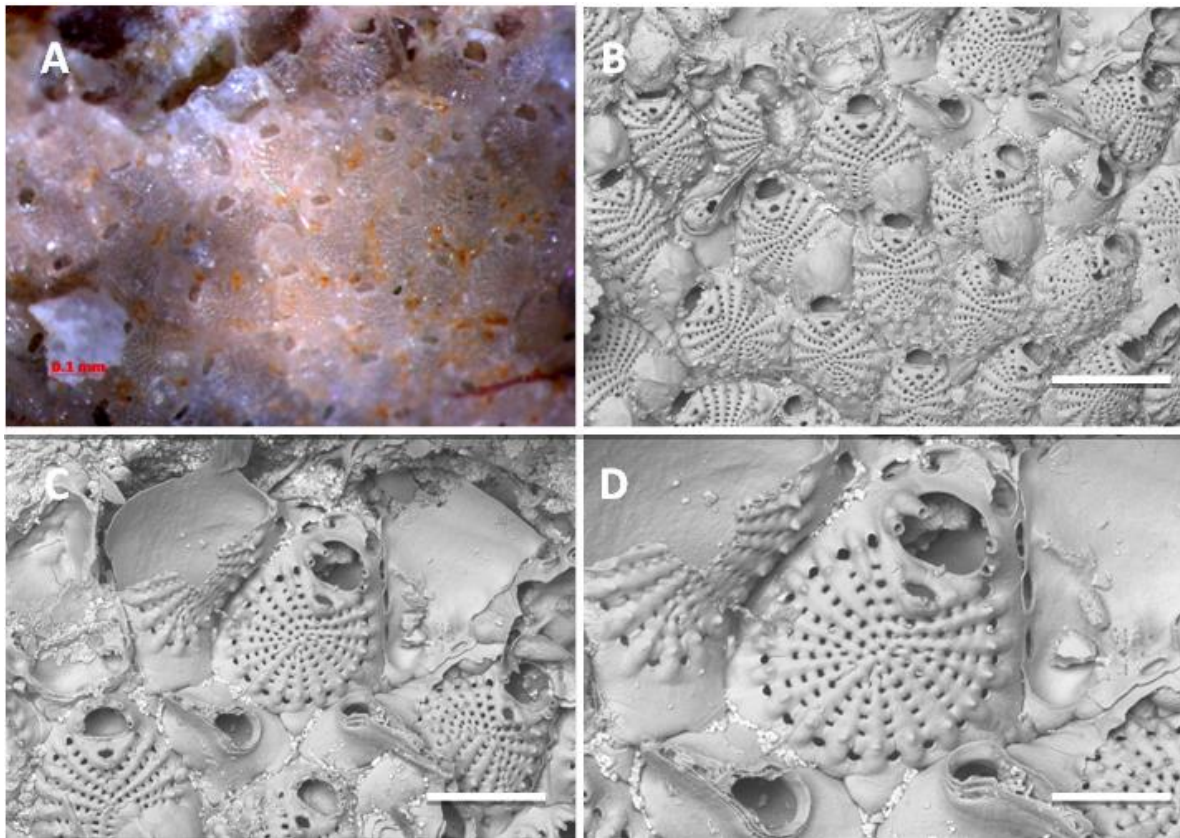


Figure 4.19: A: ZEISS microscope picture of *Puellina egretta* (scale bar= 0.1 mm), B: scanning electron micrograph of *Puellina egretta* group of ovicellate zooids at the colony margin (scale bar= 200 µm), C: a group of autozooids with interzooidal avicularia (scale bar= 100 µm), D: a close-up of a zooid orifice, oral spines, and costae (scale bar= 20 µm).

Family *Cribriliniidae* Hincks, 1879

Genus *Puellina* Jullien, 1886

Puellina egretta Ryland & Hayward, 1992

Puellina egretta – Ryland & Hayward, 1992, Tilbrook, Hayward & Gordon, 2001: p.58, Figs. 7C, D; Gluhak, Lewis & Popijac, 2007: Figs. 13A, E.

Material

Qatar: QTR-MGR-00011, collected offshore at 14m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as an irregular sheet. The autozooids are broadly oval to irregularly polygonal in shape; they are rather flat and are separated by distinct grooves. The frontal shield consists of 13 to 17 costae; each costa is broad and prominently raised at the base, and much less prominent, towards the flat central area of shield. Seven to five rather large, closely spaced, intercostal pores occur between each successive costa. The orifice is D-shaped, clearly broader than long, with a straight proximal edge. Five oral spines are present, four in ovicellate autozooids. Interzooidal avicularia are frequent; cystid, rostrum long, tapered, supporting an elongate triangular mandible. Ovicell is recumbent on distally succeeding autozooid. Ancestrula was unclear.

Table 4.13: Characteristics measurements of *Puellina egretta* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozooid length	258.5 \pm 45.1	177.8– 341.8	30
Autozooid width	195.4 \pm 31.5	145.4– 262.8	30
Orifice length	38.3 \pm 7.6	25.5 – 58.2	30
Orifice width	59.5 \pm 9.7	42.7 – 85.8	30
Ovicell length	118.3 \pm 13.3	93.6 – 154.8	19
Ovicell width	127.4 \pm 14.1	109.5 – 152.9	19
Avicularium length	211.1 \pm 19.1	193.4 – 246.1	5
Avicularium width	149.5 \pm 27.8	127.1 – 204.2	5

Remarks

Ryland and Hayward (1992) stated that the frontal shield of *Puellina egretta* is formed from about 19 fused costae (Tilbrook et al., 2001). Specimens from Green Island, Taiwan described by Gluhak et al. (2007) reported that the maximum number of fused costae forming the frontal shield is 17 matching the species described from Qatar. Three colonies were found in station 1 encrusting coral rubble. This species has been previously recorded from the Seychelles, the Philippines and Heron Island, Great Barrier Reef (Tilbrook et al., 2001). This is the first record from Qatar waters.

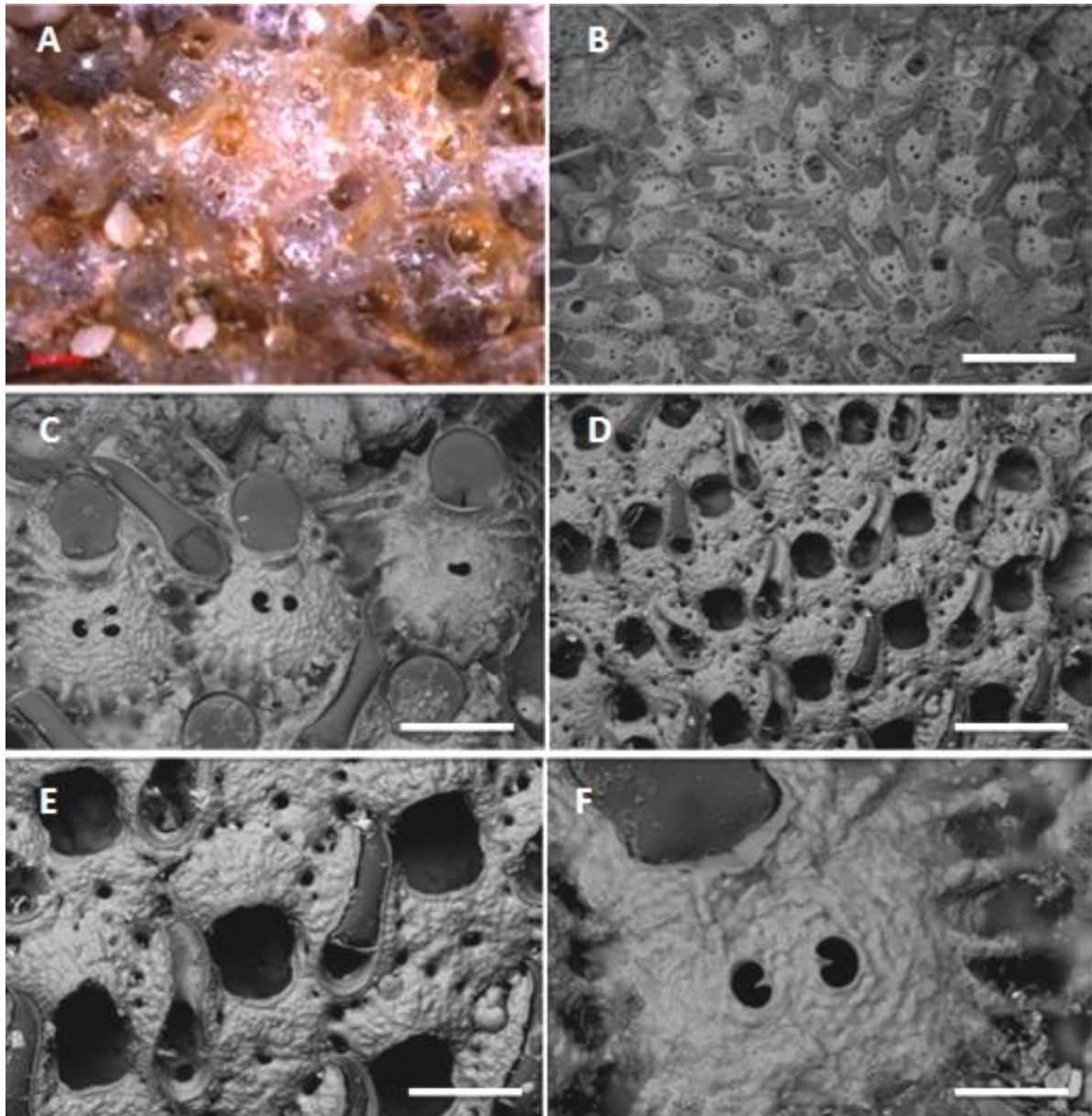


Figure 4.20: A: ZEISS microscope picture of *Poricella robusta* (scale bar= 0.2 mm), B: scanning electron micrograph of *Poricella robusta* (scale bar= 200 μm), C: close-up of a group of zooids orifice, operculum, oral spines and avicularium (scale bar= 200 μm), D: close-up of an ovicellate group of zooids (scale bar= 100 μm), E: close-up of ovicell (scale bar= 100 μm), F: close-up of ascopores (scale bar= 20 μm).

Family *Arachnopusiidae* Jullien, 1888

Genus *Poricella* Canu, 1904

Poricella robust (Hincks, 1884)

Lepraliarobusta– Hincks, 1884: p. 360, pl. 13, Fig. 4; Hincks, 1887: p. 131; Thornely, 1905: p.119; Waters, 1909: p. 152, pl. 13, Figs. 13, 14.

Tremogasterinarobusta– Powell & Cook, 1967: p. 12, pl. 1, Figs. C,D; text-Figs 1–4; Cook, 1977: p. 133, pl. 5, Fig. E, pl. 8, Figs. B,C.

Poricella robusta– Tilbrook, Hayward & Gordon, 2001: p.65, fig.10A.

Material

Qatar: QTR-MGR-00012, collected offshore at 14m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as encrusting, spreading sheets of pale yellow or orange in colour. Autozoid are oval to rectangular or hexagonal, steeply convex and separated by deep grooves. The primary orifice is bell shaped, longer than wide and slightly narrower proximally. The anter is separated by two very inconspicuous condyles. The operculum is dark brown, with a thickened marginal sclerite. Two to three long distal oral spines are present. The frontal shield is granular; large, conspicuous marginal areolae alternate with thickened ridges. One to three crescentic ascopore are present situated proximal to the orifice. A single, large spatulate avicularium occur lateral to the orifice, avicularia cystid arising from one of the areolae. The ovicell is imperforate, finely tuberculate, and initially prominent but becoming immersed.

Table 4.14: Characteristics measurements of *Poricella robusta* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	226.9 \pm 17.3	191.6 – 256.37	30
Autozoid width	135.2 \pm 28	83.3 – 183.5	30
Orifice length	89.7 \pm 9.6	68.1 – 105.6	30
Orifice width	65.1 \pm 6.3	52.77 – 81.9	30
Ovicell length	131.7 \pm 22	89.8 – 159	9
Ovicell width	218.4 \pm 31.6	160.1 – 259.6	9
Avicularium length	174.3 \pm 25.1	136.2 – 228.8	30
Avicularium width	39.1 \pm 7	26.1 – 51.2	30

Remarks

Colonies are orange in colour when alive. They were found encrusting coral rubble from station 1 and 9. The most striking feature of this species is the 1-3 central foramina on the frontal wall. This species was originally described from the Mergui Archipelago (coast of Myanmar); it has subsequently been described from the Persian Gulf, Red Sea, Seychelles and Sri Lanka (Tilbrook et al., 2001). This is the first record from Qatar waters.

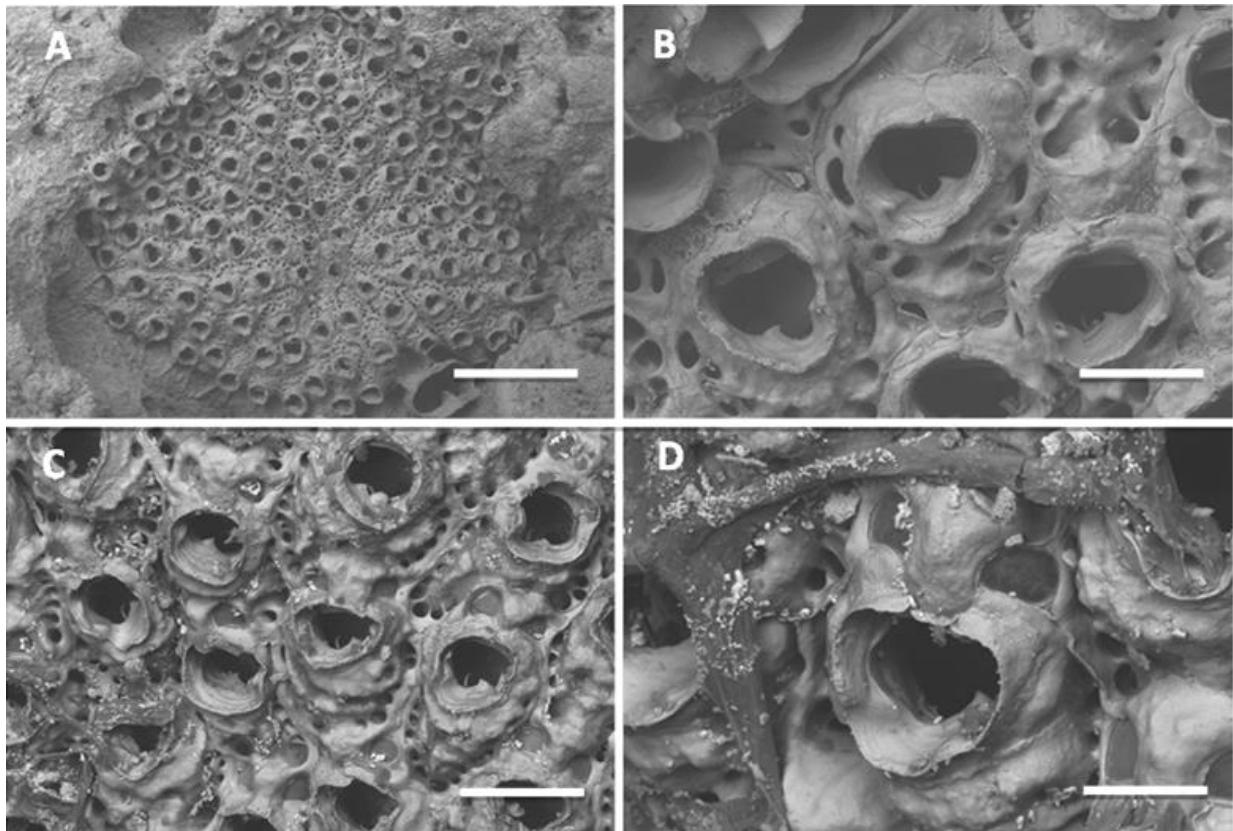


Figure 4.21: Scanning electron micrographs of *Drepanophora indica*. A: colony overview (scale bar= 200 µm), B: a close-up of autozooids orifice, peristome marginal pores and avicularium (scale bar= 100 µm), C: a group of an ovicellate zooids (scale bar= 100 µm); D: close-up of an ovicellate zooid ovicell, orifice, peristome, and avicularium (scale bar= 20 µm).

Family *Lepraliellidae* Vigneaux, 1949

Genus *Drepanophora* Harmer, 1957

Drepanophora indica Hayward, 1988

Drepanophora indica— Hayward, 1988: p. 338, pl. 14, Fig. E; Tilbrook, Hayward & Gordon, 2001: p. 73, Fig. 10C.

Material

Qatar: QTR-MGR-00013, found on coral rubble substrata, station1/sample3/colony7, collected offshore at 14m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as encrusting, pink, rounded or irregular patches. Autozooid are short, oval and strongly convex and separated by deep grooves. The frontal wall is granular with large

marginal pores. The primary orifice is longer than wide, almost pear-shaped, wider distally. The proximal border has a single transversely orientated avicularium on one side. The rostrum is sharply hooked with a slight constriction opposite. The peristome is prominent and well developed, forming a deep, flared cup around the orifice, extending onto the ovicell of the brooding autozoid. The ovicell is recumbent on the distally succeeding autozoid, prominent and globular with a large elliptical foramen, angled to frontal plane and situated either side of midline.

Table 4.15: Characteristics measurements of *Drepanophora indica* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zoids Number
Autozoid length	149.2 \pm 17.4	114 – 192	30
Autozoid width	94.3 \pm 10.6	68.1 – 111.1	30
Orifice length	58.9 \pm 11.1	39.6 – 92.2	30
Orifice width	66.2 \pm 7	49.4 – 79.2	30
Ovicell length	169.5 \pm 38.4	88.5 – 214.4	9
Ovicell width	290.5 \pm 35.8	244 – 357.5	9

Remarks

Hayward (1988) distinguished *Drepanophora indica* from *Drepanophora uerrucosa* described by Winston & Heimberg (1986) using criteria of the ovicell and orificial avicularium. The most distinguished characteristic is the large elliptical foramen, angled to frontal plane, on either side of the midline of the ovicell. Tilbrook et al. (2001) recorded a single ovicellate colony from the Island of Efate, Vanuatu which was compared to the Hayward (1988) type specimen. The Qatar material matches the description of *Drepanophora indica*. In Qatar seven colonies of this species were found in station 1, 2, and 5 on coral rubble. This is the first record for this species in Qatar waters.

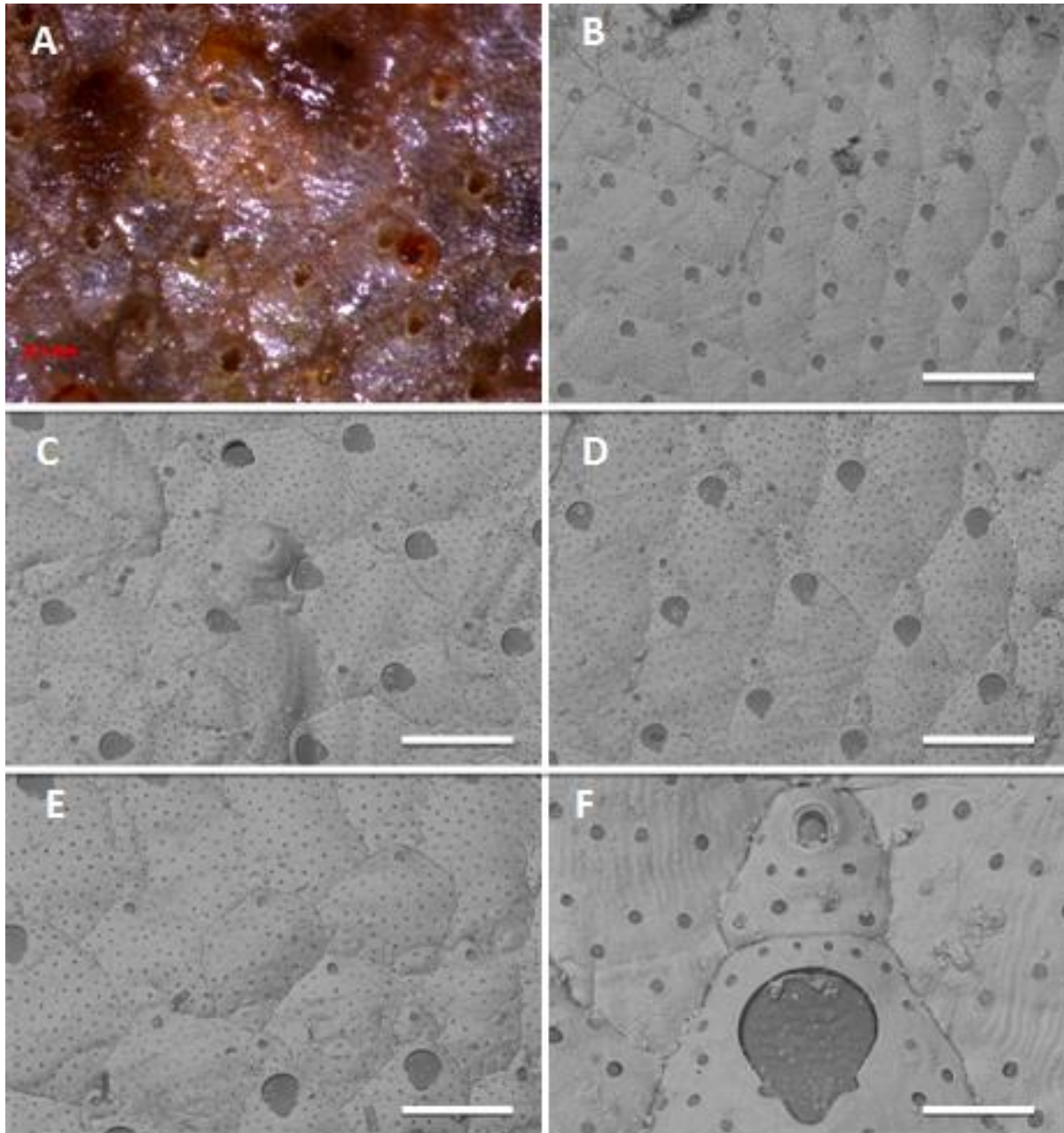


Figure 4.22: A: ZEISS microscope picture of *Trypostega johnsoulei* (scale bar= 0.1mm), B: scanning electron micrograph of *Trypostega johnsoulei* (scale bar= 200 µm). C: a group of an ovicellate zooids (scale bar= 200 µm), D: a group of autozooids and kenozooids (scale bar= 100 µm) E: a group of kenozooids (scale bar= 100 µm); F: close-up of a zooid orifice, operculum, and kenozooid (scale bar= 10 µm).

Family *Trypostegidae* Gordon, Tilbrook & Winston, 2005

Genus *Trypostega* Levinsen, 1909

Trypostega johnsoulei Tilbrook, 2006

Trypostega johnsoulei – Tilbrook, 2006: p.112, pl. 18C, D.

Material

Qatar: QTR-MGR-00014, collected offshore at 15m depth, found on pearl oyster shell *Pinctada radiata* substrata (Appendix J).

Description

Colony grows as encrusting thin sheets. The autozooids are diamond shaped to irregularly polygonal, convex and separated by shallow grooves. The frontal shield is smooth and perforated by numerous (70-90) round small pores. The orifice is pear shaped, longer than wide, orbicular anter, poster rounded and bowl shaped. The condyles are short and triangular. The operculum is dark brown and distinct. The ovicell is hyperstomial, prominent, oval or irregular, finely granular. Kenozooids are distal to all autozooid and ovicells; orifice of kenozooids is small, anter deep, and mandible rounded (Tilbrook, 2006).

Table 4.16: Characteristics measurements of *Trypostega johnsoulei* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozooid length	361.2 \pm 30.7	290 – 413.5	30
Autozooid width	207.5 \pm 24.6	149.2 – 260.6	30
Orifice length	58.5 \pm 4.4	48.3 – 67.1	30
Orifice width	53.5 \pm 3.2	45.6 – 60.1	30
Ovicell length	265.9 \pm 34.6	234.1 – 332.3	5
Ovicell width	264.3 \pm 22.1	240 – 306.1	5
Kenozooids length	71.3 \pm 14.8	50.9 – 111.5	30
Kenozooids width	63.2 \pm 7.2	50.3 – 77.6	30

Remarks

Trypostega species is characterised by its primary orifice, and frontal shield that is sparsely perforated by pores (Tilbrook, 2006). *Trypostega* species from Qatar matched *Trypostega johnsoulei* by Tilbrook (2006) in the number of pores in the frontal shield (70-90) and in zooid size; *Trypostega johnsoulei* from the Solomon Islands measured an average of 384.1 μm in length (range: 318.57 - 421) and 186.9 μm in width (range: 150.38 - 245.6). The ovicell of *Trypostega johnsoulei* was not observed in Tilbrook (2006) specimen. *Trypostega* species from Qatar differs from *Trypostega venusta* (Norman, 1864) for the absence of the umbo that is proximal to the orifice. *Trypostega* species from Qatar also differs from

Trypostega henrychaneyi (Tilbrook, 2006) in the number pores in the frontal shield; *Trypostega henrychaneyi* contains (80-100) pores.

In Qatar forty seven colonies of this species were found across all stations encrusting coral rubble, shells and pearl oyster shells *Pinctada radiata*, but almost half of the colonies numbers were recorded from station 1; twenty five colonies. *Trypostega johnsoulei* was only found in the Solomon Islands (Tilbrook, 2006). This is the first time this species has been recorded from Qatar coastal waters.

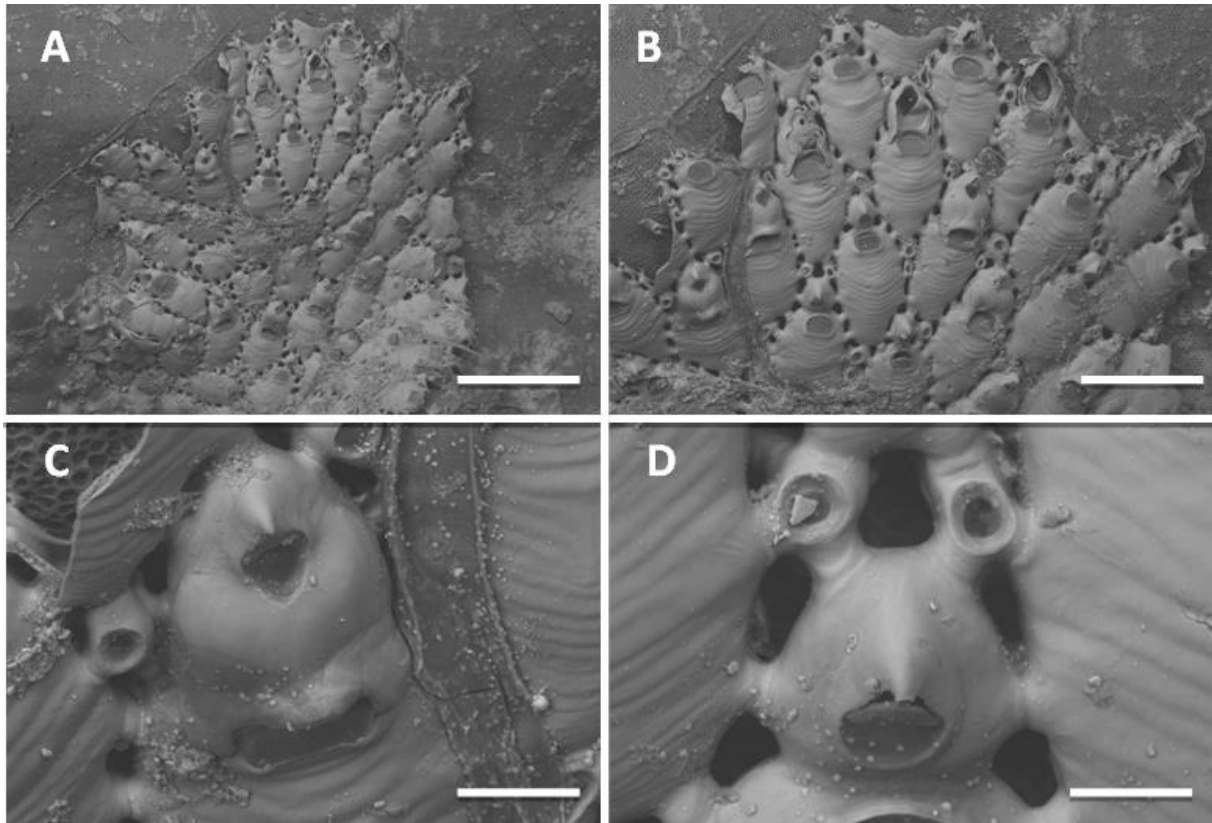


Figure 4.23: Scanning electron micrographs of *Chorizopora brongniartii*. A: colony overview (scale bar= 200 μm), B: close-up of a single zooid orifice, operculum, kenozooids and avicularium (scale bar= 100 μm), C: close-up of ovicell, avicularium and kenozooid (scale bar= 20 μm), D: close-up of avicularium (scale bar= 10 μm).

Family *Chorizoporidae* Vigneaux, 1949

Genus *Chorizopora* Hincks, 1879

Chorizopora brongniartii (Audouin, 1826)

Flustra brongniartii – Audouin, 1826: p. 240, pl. 10, Fig. 6.

Chorizopora brongniartii –Hincks, 1880: p. 224, pl. 32, Figs. 1-4; Hayward & Ryland, 1999: p. 100- 101, Figs. 24C, D; 25; Tilbrook, 2006: p.101, pl.12 B-D.

Material

Qatar: QTR-MGR-00015, collected offshore at 20 m depth, found encrusting on coral rubble substrata (Appendix J).

Description

Colonies form broad spreading sheets, thin and translucent. Autozooids are oval, occasionally pear-shaped or irregular, separated by shallow grooves. Adjacent autozooids linked by short tubules, extensions of the pore chambers. Frontal wall smooth marked with ridges. The Orifice is wider than long, semicircular, sub-terminal, with a thin rim and no peristome. Avicularia cystid small, linked to adjacent autozoid by communication tubes, mandible at an acute angle to the frontal plane, triangular, directed distally. A single avicularium situated distal to each zoid. Small irregularly shaped kenozooids, linked by tubules to surrounding autozooids; generally small with circular or oval orifice but no operculum. Ovicell prominent, hyperstomial, smooth; the distal avicularium closely associated with the ovicell.

Table 4.17: Characteristics measurements of *Chorizopora brongniartii* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zoids Number
Autozoid length	183.9 \pm 32.9	103.2 – 232	30
Autozoid width	112.3 \pm 14.1	81.2 – 147	30
Orifice length	35.4 \pm 4.4	29.1 – 46.4	30
Orifice width	45.6 \pm 8.8	29.8 – 61.1	30
Ovicell length	79.5 \pm 8.3	65.6 – 98.6	19
Ovicell width	86.4 \pm 6.8	74.8 – 96.7	19
Avicularium length	48.6 \pm 10.4	32.5 – 66.1	23
Avicularium width	48.2 \pm 8	34 – 61.8	23
kenozooids length	60 \pm 15.5	48.9 – 16 .3	21
kenozooids width	29.8 \pm 108.6	21.7 – 91.3	21

Remarks

Only one colony of *Chorizopora brongniartii* species was found from Qatar encrusting on coral rubble in station 7. *Chorizopora brongniartii* is widely distributed in both temperate and tropical shelf seas (Tilbrook, 2006). Autozooids of *Chorizopora brongniartii* species from Qatar are smaller in size than *Chorizopora brongniartii* from Isle of Man, autozoid mean length and width 262.6 μm and 181.5 μm . Both species of *Chorizopora brongniartii* from Isle of Man and Qatar had the same characteristic features. However, ovicells were not seen in Isle of Man specimen.

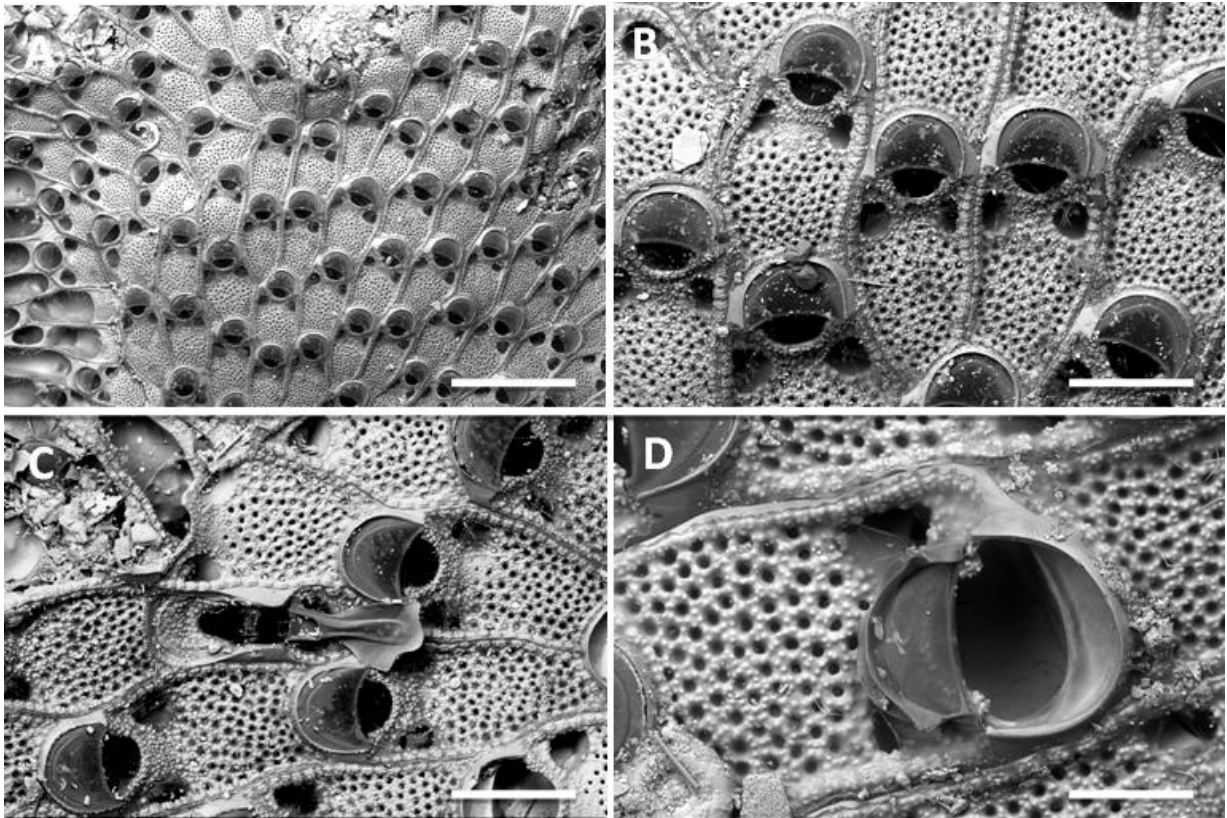


Figure 4.24: Scanning electron micrographs of *Thalamoporella granulata*, A: colony overview (scale bar= 200 µm), B: close-up of a group of zooids orifice and operculum (scale bar= 100 µm), C: close-up of avicularium with open mandible (scale bar= 100 µm), D: close-up of a group of zooids orifice, operculum, and condyles (scale bar= 100 µm).

Suborder *Thalamoporellina*

Family *Thalamoporellidae* Levinsen, 1902

Genus *Thalamoporella* Hincks, 1887

Thalamoporella granulata Levinsen, 1909

Thalamoporella granulata var. *B* – Levinsen, 1909: p190, Fig. 6A, Figs. 1A-F.

Thalamoporella granulata –Harmer, 1926: p. 297; Hayward & Ryland, 1992: p. 241, Fig. 11A-B; Soule, Soule & Chaney, 1992: p. 48, Figs. 66-68; Tilbrook, Hayward & Gordon, 2001: 55; Tilbrook, 2006: p.87, pl.12 D.

Material

Qatar: QTR-MGR-00016, collected offshore at 14.2m depth, found on coral rubble substrata (Appendix J).

Description

Colony grows as encrusting unilaminar sheet. Autozooids are almost rectangular, distinct and separated by shallow grooves. The gymnocyst is reduced, present as a narrow margin. The cryptocyst is granular, reaching two-thirds the way around either side of the orifice, it is punctured frontally by irregularly spaced pores. Opsiules are irregularly oval and unequal in size. The orifice is rounded, slightly longer than wide, distal rim raised slightly, with small triangular, lateral condyles positioned at edge of cryptocyst. Autozooids are shorter than the avicularia. Avicularia are uncommon, torqued towards sibling zooid, rostrum rounded toward sibling with smooth distal platform, distally directed mandible sub-spatulate, cryptocyst finely granular. Ovicells are absent (Tilbrook, 2006).

Table 4.18: Characteristics measurements of *Thalamoporella granulata* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozooid length	292.1 \pm 38.5	214.6 – 372.5	30
Autozooid width	155.8 \pm 38.2	100.5 – 291.1	30
Orifice length	87.5 \pm 12.7	51.2 – 108.9	30
Orifice width	83.2 \pm 9.1	50.2 – 100.8	30
Avicularium length	383.1 \pm 0	383.1– 383.1	1
Avicularium width	144.9 \pm 0	144.9 – 144.9	1
Mandible length	217.5 \pm 0	217.5 – 217.5	1
Mandible width	104.6 \pm 0	104.6 – 104.6	1

Remarks

Thalamoporella species have distinctive morphological features these include the shape and orientation of the avicularia and the ratios of autozooid to avicularium lengths are important for species identification and differentiation (Tilbrook, 2006). *Thalamoporella granulata* from Qatar has a large spatulate avicularia that has torqued avicularia/sibling zooid arrangement. The avicularium is slightly longer than the autozooid. In Qatar one colony of this species was found in Station 9 encrusting coral rubble substrata. *Thalamoporella granulata* was originally described from Torres Strait (Levinsen, 1909) and it has a wide distribution within the Indo-West Pacific. It has been recorded from the Seychelles, Indonesia, the Philippines, Great Barrier Reef, Solomon Islands, Vanuatu, Fiji, Tonga, and from the Pliocene of Taiwan. Tilbrook (2006) found this species in Mbanika Island, Russell Islands, while Soule et al. (1992) recorded it from the same locality and Anuha Island as well

as Florida Islands (Tilbrook, 2006). This is the first time this species has been recorded from Qatar coastal waters.

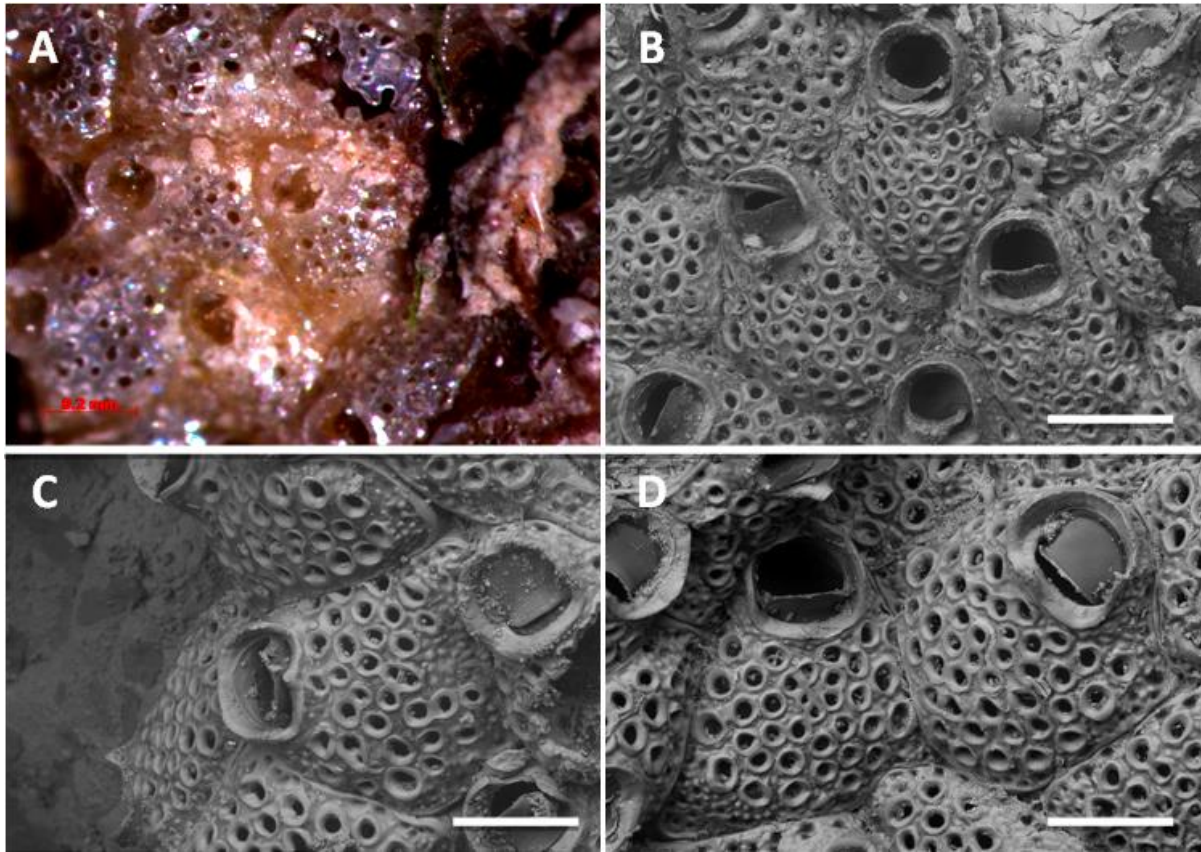


Figure 4.25: A: ZEISS microscope picture of *Exechonella brasiliensis* (scale bar= 0.2 mm), B: Scanning electron micrograph of a group of zooids (scale bar= 200 µm), C: close-up of zooids peristome umbo (scale bar= 100 µm), D: close-up of a group of zooids orifice, operculum, peristome and frontal shield foramina (scale bar= 100 µm).

Family *Exechonellidae* Harmer, 1957

Genus *Exechonella* Duvergier, 1924

Exechonella brasiliensis Canu & Bassler, 1928

Exechonella brasiliensis – Canu & Bassler, 1928: p.72; Winston & Heimberg, 1986: p. 15, Figs 26, 27; Winston, 1986: p. 19; Scholz, 1991: p. 289, pl. 7, Fig. 1; Tilbrook, Hayward & Gordon, 2001: p.65, Fig.8G.

Material

Qatar: QTR-MGR-00017, collected offshore at 14.2m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as encrusting, unilaminar small patches. Autozooids are oval, convex and separated by deep grooves. The primary orifice has a cylindrical peristome. The frontal shield has 30-40 round foramina, each with a thick raised, more or less circular rim; peristome finely nodular, cylindrical, with a slightly flared rim, up to 0.034 mm long. Peristome developed laterally and proximally with an umbo. No avicularia are present.

Table 4.19: Characteristics measurements of *Exechonella brasiliensis* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	249.6 \pm 37.6	123.4 – 301.5	30
Autozoid width	175 \pm 38.4	88.4 – 270.52	30
Orifice length	58.7 \pm 8.1	43 – 71.6	30
Orifice width	66.8 \pm 8.2	48.14 – 81.4	30
Peristome length	34.3 \pm 6	23.6 – 44	19

Remarks

The most striking feature of this species is the numerous round foramina on the frontal shield. Five colonies of this species were found in Qatar, 4 colonies were recorded from station 1 and 1 colony was recorded from station 9. Winston & Heimberg (1986) give a very comprehensive description and discussion of this species, having found a single colony in their samples from Indonesia. As its name suggests this species was originally described from Brazil (Canu and Bassler, 1928) and several colonies were found at both Iririki Island and Port Vila Harbour on small pieces of coral rubble and discarded wall tiles. This record establishes the presence of this species in the Southwest Pacific area (Tilbrook et al., 2001). This is the first record for this species in Qatar coastal waters.

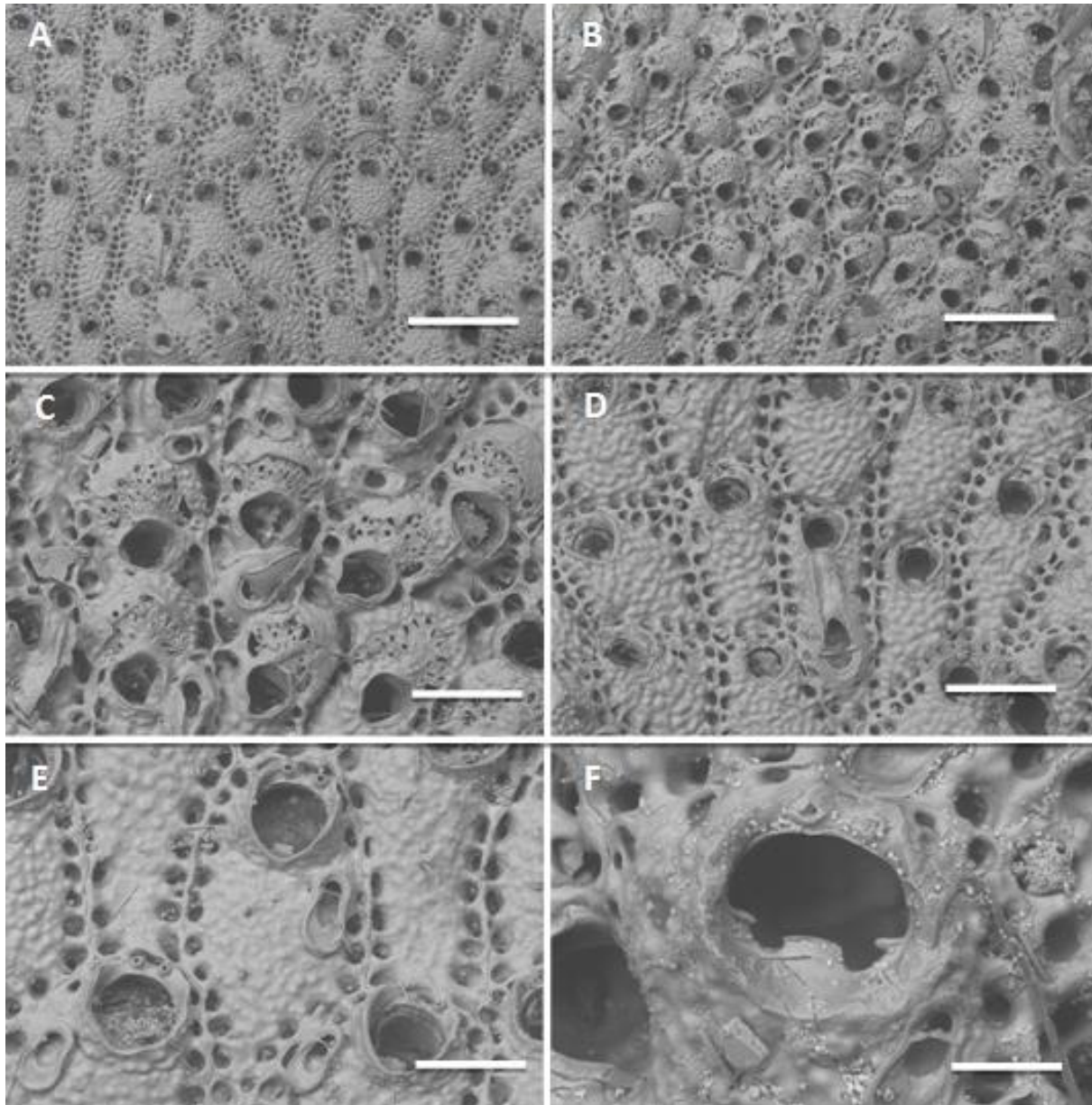


Figure 4.26: Scanning electron micrographs of *Parasmittina raigii*. A: a group of autozooids at the colony margin (scale bar= 200 µm), B: a group of an ovicellate zooids (scale bar= 200 µm), C: close-up of an ovicellate zooids with different types of avicularia (scale bar= 100 µm), D: a group of autozooids (scale bar= 100 µm), E: close-up of a group of zooids orifice, lyrula, oral spines, marginal pores, avicularia and peristome (scale bar= 100 µm), F: close-up of zooid orifice, lyrula, oral spines, marginal pores, and pointed condyles (scale bar= 10 µm).

Family *Smittinidae* Levinsen, 1909

Genus *Parasmittina* Osburn, 1952

Parasmittina raigii (Audouin, 1826)

Cellepora raigii – Audouin, 1826: p. 238.

Smittina raigii – Harmer, 1957: p. 938-940.

Parasmittina raigii – Gautier, 1962: p. 198, 199, Arístegui, 1984: p. 265-267, Fig. 55E-G, pl. 16, Figs. 1, 5, Zabala & Maluquer, 1988: p. 119, Fig. 252, Hayward & Parker, 1994: p. 71-73, Figs. 6F, 7A, B., Koçak et al. 2002: p. 236; Harmelin, Bitar, & Zibrowius, 2009: Fig. 4 A, E.

Material

Qatar: QTR-MGR-00018, collected offshore at 15m depth, found on pearl oyster shell *Pinctada radiata* substrata (Appendix J).

Description

Colony grows as encrusting sheets which are often nodular and yellowish-white in colour. Autozooids are elongate, quadrate to oval, flat or slightly convex and separated by distinct sutures. The frontal shield is granular. The primary orifice is orbicular, with a short, quadrate lyrula. Condyles are pointed, and the peristome is erect, thin, enclosing the proximal and lateral borders, extending onto the ovicell, so forming a complete tube; with a deep slit proximally. Two distal oral spines are present, these are short and slender. Adventitious avicularia are situated lateral to the orifice, directed distally or distolaterally, away from the orifice or towards it, encroaching on the peristome; mandible acutely triangular. Other avicularia are present, additional to or replacing the lateral oral type, usually smaller, closely associated with the areolae. The ovicell is spherical, recumbent on the distal autozoid, often partly covered by coarser calcification from the distal autozoid; with large, irregular shaped frontal pores.

Table 4.20: Characteristics measurements of *Parasmittina raigii* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	289.4 \pm 47.6	187.8 – 395.5	30
Autozoid width	190.2 \pm 26.46	142.2 – 250.6	30
Orifice length	61.5 \pm 5.7	51.5 – 73.9	30
Orifice width	67.3 \pm 5.4	54.4 – 75.7	30
Ovicell length	107.4 \pm 13.9	76.3 – 152.5	30
Ovicell width	153.1 \pm 15.7	107.4 – 176.5	30
Big avicularium length	168.6 \pm 49.3	117.7 – 257.1	8
Big avicularium width	61.9 \pm 16.2	40 – 94.1	8
Small avicularium length	71.2 \pm 10.9	49.5 – 95.7	18
Small avicularium width	36.1 \pm 5.9	26.1 – 49.4	18

Remarks

Harmelin, et al., (2009) stated that in specimens of *Parasmittina raigii* from Lebanon the primary orifice has 2-3 spines and a denticulate distal rim. Specimens from Qatar have only 2 spines and no denticulate distal rim around the orifice. However, the lyrula and condyles do match the Harmelin et al. (2009) description. *Parasmittina raigii* was found in station 1, 2, and 3 encrusting pear oyster shells *Pinctada radiata*.

Specimens from Syria first assigned to *Smittina trispinosa* by Gautier (1956) were afterwards placed in synonymy with *Parasmittina raigii* by Gautier (1962), who also recorded species from Algeria, Corsica and the French Riviera. *Parasmittina raigii* is widespread in warm temperate and tropical regions (Harmelin et al., 2009). These are the first records from Qatar coastal waters.

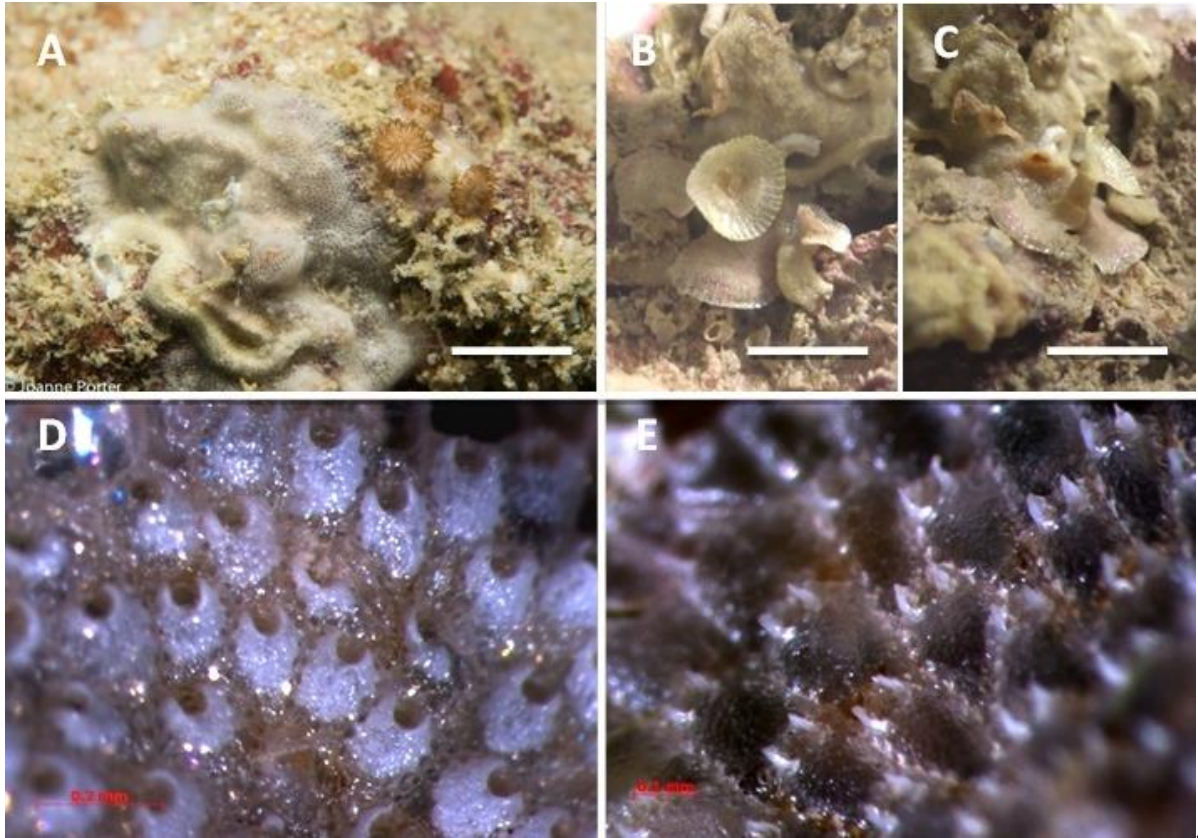


Figure 4.27: A, *Parasmittina egyptiaca* encrusting coral (scale bar= 1 cm), B, C: *Parasmittina egyptiaca* encrusting around worm calcified tube (B: scale bar= 1.5 cm, C: scale bar= 2 cm), D: ZEISS microscope picture of secondary calcification on the zooid frontal shield (scale bar= 0.2 mm), E: ZEISS microscope picture of wings shaped peristome (scale bar= 0.1 mm).

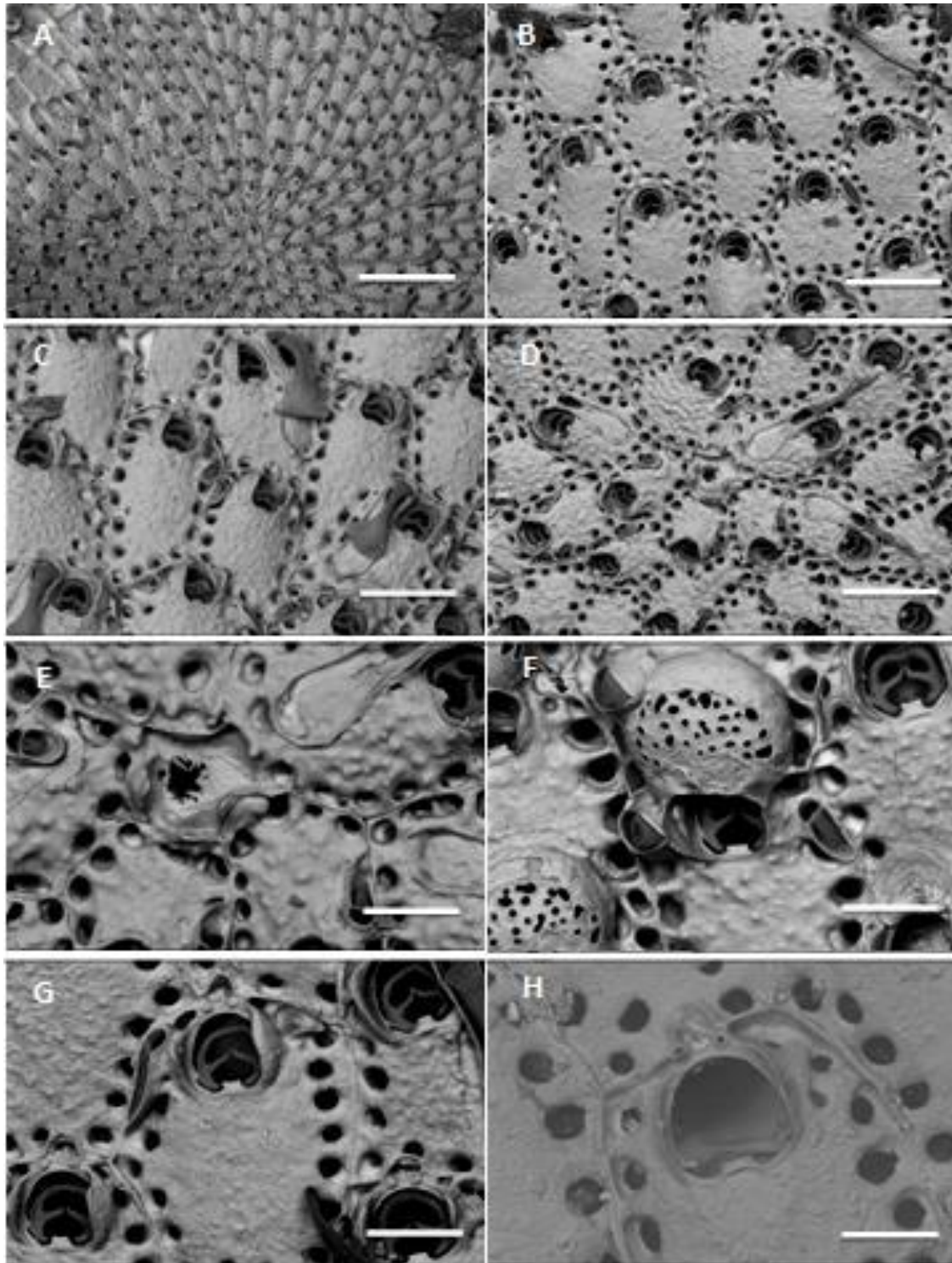


Figure 4.28: Scanning electron micrographs of *Parasmittina egyptiaca* from Qatar. A: colony overview (scale bar= 200 µm), B: a group of autozooids at colony margin (scale bar= 100 µm), C: a group of autozooids with spatulated adventitious avicularia (scale bar= 100 µm), D: a group of ancestrula zooids (scale bar= 200 µm); E: close-up of ancestrula, frontal membrane with denticulation (scale bar= 20 µm), F: close-up of an ovicellate zooid (scale bar= 20 µm), G: close-up of a group of zooids orifice, lyrula, oral spines, marginal pores, peristome, avicularia and operculum marked with distinct patterns (scale bar= 20 µm), H: close-up of an open orifice with lyrula, and pointed condyles (scale bar= 20 µm).

Parasmittina egyptiaca (Waters, 1909)

Smittia egyptiaca –Waters, 1909: p. 157, pl. 15, Figs 6, 9 (Red Sea), Hastings, 1927: p. 342-345, Fig. 85-87; Harmer, 1957: p. 937, 938, pl. 64, Figs. 21, 22, 29-31.

Parasmittina egyptiaca – Powell, 1967: p. 171, pls. 3, 13, Powell, 1969: p. 361, Fig. 4; Harmelin, Bitar, & Zibrowius, 2009: Fig. 2 A, E.

Material

Qatar: QTR-MGR-00019, collected offshore at 15m depth, found on pearl oyster shell *Pinctada radiata* substrata (Appendix J).

Description

Colony grows as an encrusting yellow-white spreading patch, or rising from the substrata; either unilaminar, or multilaminar with autozooids in contact basally. Autozooids are elongate, quadrate to oval, flat or slightly convex and separated by distinct sutures. The frontal shield is granular with large marginal pores. The primary orifice is orbicular with a short, quadrate lyrula. Condyles are pointed and the operculum is marked with distinct patterns. The peristome is prominent, erect, thin, forming paired lateral wings and incomplete proximally. In fertile autozooids they extend onto the frontal surface of the ovicell. Two distal oral spines, occur, these are short and slender. Single, large, spatulate adventitious avicularia, situated lateral to the orifice, along the right, or left side of autozooid, mandible spatulate. Other avicularia present: paired, lateral to the orifice, cystid small, not globular; mandible slender. The ovicell is spherical, prominent, and recumbent on the distal autozooid, often partly covered by coarser calcification from the distal autozooid; with large, round or irregular shaped frontal pores. The ancestrula is irregularly shaped, with frontal membrane surrounded by distinct denticulation, and budding of five autozooids.

Table 4.21: Characteristics measurements of *Parasmittina egyptiaca* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	185 \pm 42.5	120.7 – 325.4	30
Autozoid width	118.8 \pm 14.9	88.2 – 158.9	30
Orifice length	46 \pm 7.5	32.8 – 63.7	30
Orifice width	40.9 \pm 4.4	32.9 – 49.6	30
Ovicell length	202.4 \pm 54.6	121 – 22.1	6
Ovicell width	250.6 \pm 66.5	142.9 – 303.8	6
Big avicularium length	132.2 \pm 28.7	68 – 174.9	15
Big avicularium width	33.3 \pm 8	14 – 42.1	15
Small avicularium length	39.4 \pm 7.2	24.6 – 57.2	30
Small avicularium width	20.1 \pm 3.7	11.4 – 27.5	30
Mandible length	106.5 \pm 28.6	46.2 – 148.1	15
Mandible width	21.3 \pm 7	9.6 – 31.9	15
Ansestrula length	75.5 \pm 53.2	37.8 – 113.2	2
Ansestrula width	37 \pm 18.3	24 – 50	2

Remarks

This species is characterised first by constant features of the orifice. The low, lateral flaps of the peristome which flank the two distal spines are typical, as is the primary orifice, which is entirely visible frontally, invariably with a square-rounded outline and a low, broad lyrula with straight distal edge and concave lateral sides. The shape of the condyles is also highly diagnostic.

The giant avicularium is a diagnostic feature, particularly the distal rim of the rostrum with paired, pointed blades. These flaps are sometimes lower, less pointed or even absent and, in the latter case; the distal end of the rostrum is spoon-shaped. The position of the giant avicularium, against the orifice and sometimes very distal, and the small size of its foramen is also characteristic.

Smittina egyptiaca described by Waters (1909) show regularly arranged autozooids, with a nodular frontal shield and delimited marginal pores, sub-quadrate primary orifices, with a wide, quadrate lyrula, and small, pointed avicularia lateral to the orifice. These characters are typical of the Lebanese specimens from Harmelin et al. (2009), and the main difference would be the lack of large spatulate avicularia in the material examined by Waters. However,

giant avicularia were present in the Qatar species. Electron micrographs of *Parasmittina egyptiaca* from Lebanon (Harmelin et al., 2009) show autozooids very similar to the Qatar ones.

A specimen from Port-Said Egypt, illustrated by Hastings (1927) and a specimen from Massawa, S Red Sea by Powell (1967: pl. 3, Fig. 13, 1969) of *Parasmittina egyptiaca* all shows the same type of orifice, numerous small avicularia with pointed rostrum and a giant spatulate avicularium.

Parasmittina egyptiaca species were dominant in Qatar and colonies were recorded 128 times across all stations encrusting coral rubble and 74 times encrusting on 50 pear oyster shells *Pinctada radiata*. *Parasmittina egyptiaca* was recorded early in the Suez Canal by Hastings (1927), from Port Taufiq (Suez side entrance) to the Great Bitter Lake but had not yet been recorded in the Mediterranean (Harmelin et al., 2009).

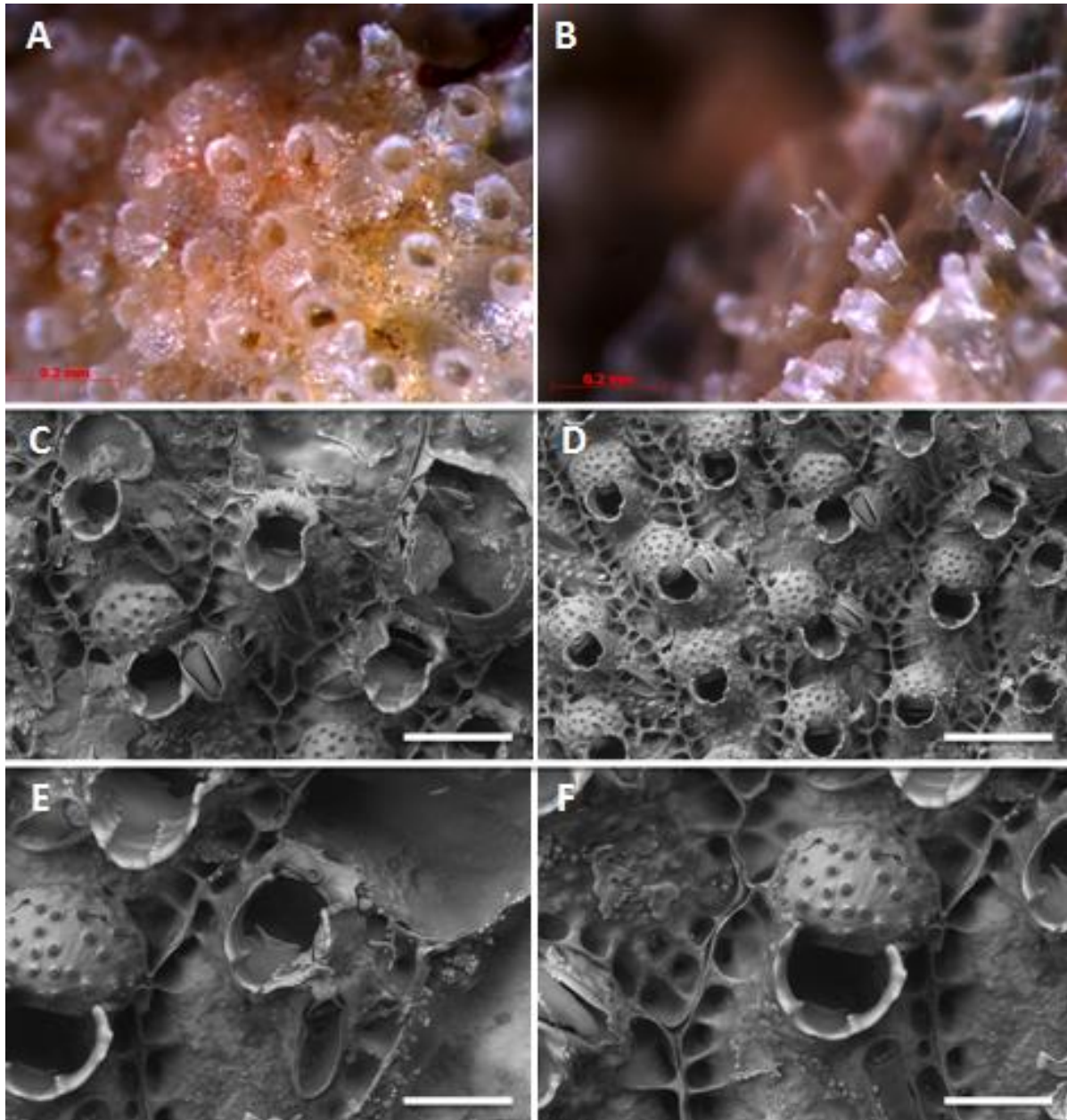


Figure 4.29: A: ZEISS microscope picture of *Parasmittina spondylicola* colony overview (scale bar= 0.2 mm), B: ZEISS microscope picture of side view of spine and peristome (scale bar= 0.2 mm), C: scanning electron micrograph of *Parasmittina spondylicola* colony edge (scale bar= 100 μ m), D: close-up of an ovicellate group of zooids (scale bar= 100 μ m), E: close-up of zooid orifice, lyrula, oral spine, peristome and avicularium (scale bar= 20 μ m), F: close-up of ovicell, peristome, and marginal pores (scale bar= 20 μ m).

Parasmittina spondylicola Harmelin, Bitar & Zibrowius, 2009

Parasmittina sp. – Sternhell et al, 2002: p. 226, Fig. 3E, F.

Parasmittina tropica – Scholz, 1991: p. 327, pl. 19, Fig 5-7.

Parasmittina aff. *tropica* – Ristedt & Hillmer, 1985: p. 138, pl. 4, Fig. 8.

Parasmittina spondylica –Harmelin, Bitar, & Zibrowius, 2009: Fig. 7 A, D.

Material

Qatar: QTR-MGR-00020, collected offshore at 16.8m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as small, encrusting, round patches. Autozooids are oval, convex and separated by shallow grooves. The frontal shield is granular with large marginal pores. The primarily orifice is orbicular with an anvil-shaped lyrula. Condyles are small. One distal oral spine is present. The peristome is tall and cylindrical, enclosing the orifice proximally and laterally; its rim is slightly flared, produced into a number of short, blunt processes. A spatulated avicularia is situated immediately proximal to peristome. The ovicells are frequent, rounded, wider than long, and have pores distributed on the whole frontal area.

Table 4.22: Characteristics measurements of *Parasmittina spondylica* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	252.1 \pm 25.8	211.9 – 311	28
Autozoid width	159.7 \pm 31	103.7 – 218.2	28
Orifice length	63.3 \pm 12.7	42.2 – 102.3	28
Orifice width	66.3 \pm 10.2	47.7 – 88.5	28
Ovicell length	87.3 \pm 9.7	67.7 – 112.5	19
Ovicell width	105.6 \pm 27	61 – 133.5	19
Avicularium length	90.2 \pm 10.4	66.8 – 104.5	17
Avicularium width	26.8 \pm 5.8	16 – 34.3	17

Remarks

The most striking distinctive features in this small and delicate species are the single orifice spine, high tubular peristome interrupted distally, and the adventitious avicularium with relatively narrow, slightly spatulate rostrum and round tip. The frequency of ovicells, which are clearly prominent and not obscured by secondary calcification, is also typical of this species and may indicate a reproductive strategy adapted to opportunistic colonisation of free spaces and short life duration (Harmelin et al., 2009).

In total eight colonies of *Parasmittina spondylicola* species were recorded across the coastline of Qatar, five colonies from station 1, and one colony from station 2, 5, and 7. This species was found encrusting on coral rubble substrata. *Parasmittina spondylicola* was recorded from the Mediterranean in Lebanon and the Gulf of Aqaba, and also from the Philippines Islands (Harmelin et al., 2009).



Figure 4.30: Image of *Schizoporella errata* in situ (scale bar= 10 cm).

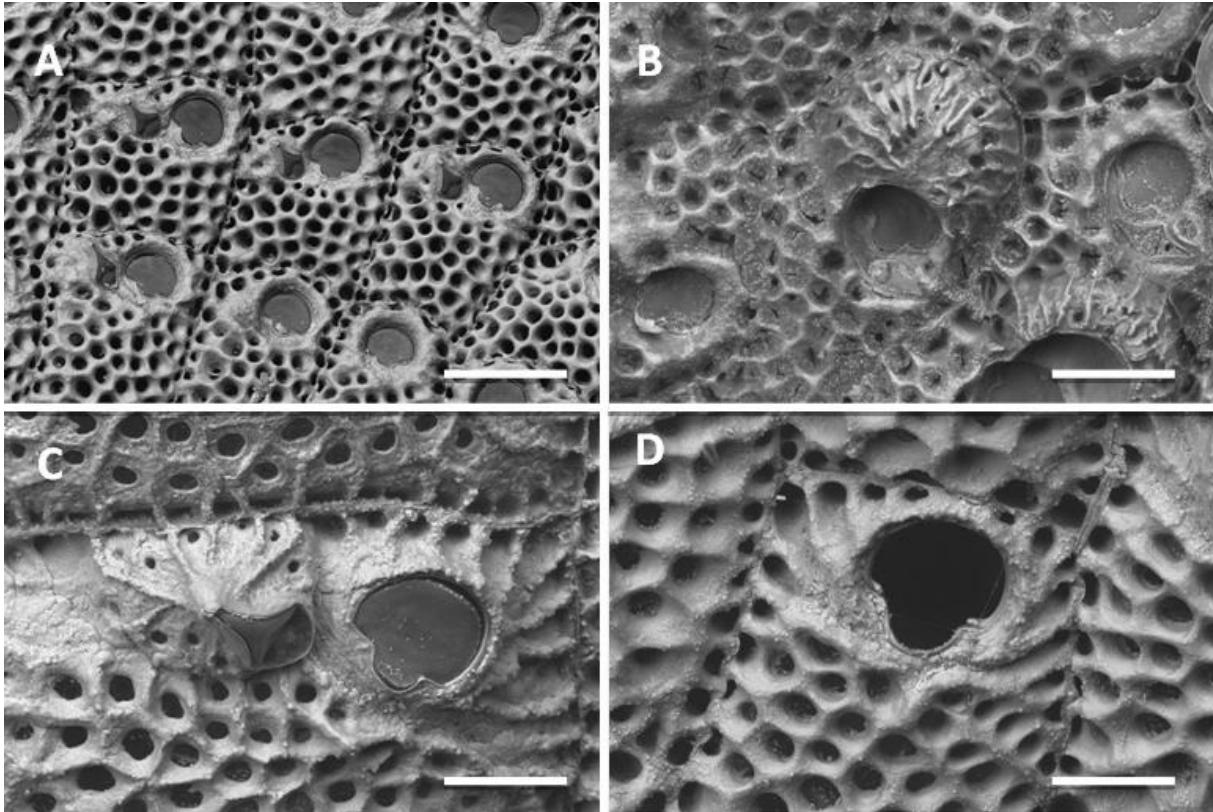


Figure 4.31: Scanning electron micrographs of *Schizoporella errata*. A: close-up of a group of zooids orifice, operculum, frontal shield pores and avicularium (scale bar= 200 μ m), B: close-up of ovicell (scale bar= 100 μ m), C: extra close-up of zooid orifice, operculum and avicularium (scale bar= 20 μ m), D: close-up of an open orifice with pointed condyles (scale bar= 20 μ m).

Family *Schizoporellidae* Jullien, 1883

Genus *Schizoporella* Hincks, 1877

Schizoporella errata (Waters, 1878)

Lepralia errata – Waters, 1878: p.11, pl. 1, Fig. 9; Waters, 1878: p.11, pl. 1, Fig. 9. Fig. 68; Brock, 1985: p.46, Fig. 2C; Gordon & Mawatari, 1992: p.31, pl. 9, Fig. B.

Schizoporella violacea – Canu and Bassler, 1930: 44, pl.4, Figs. 1-14.

Schizoporella unicornis – Marcus, 1940: p. 237, Fig. 121.

Schizoporella errata – Hayward and Ryland, 1999: p.212, Fig. 86; Tilbrook, Hayward & Gordon, 2001: p.80, fig.15B.

Material

Qatar: QTR-MGR-00021, collected offshore at 20m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as encrusting, unilaminar or multilaminar spreading sheets, or erect; whitish-pink to violet-brown in colour. Autozooids are rectangular, flat or slightly convex and separated by shallow grooves. The frontal shield is evenly perforated by numerous round pores. The primary orifice is slightly wider than long, appearing almost circular; with a broad shallow U-shaped median sinus. There are no oral spines. The adventitious avicularium is single, situated lateral to the orifice and level with the proximal border or sinus; cystid prominent, mandible acute triangular, angled to frontal plane, distolaterally orientated. Ovicells are prominent, globular, regularly perforated by small round pores, and with a much ridged surface (Tilbrook et al., 2001).

Table 4.23: Characteristics measurements of *Schizoporella errata* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	295.6 \pm 29.8	242.2 – 338.3	25
Autozoid width	253.8 \pm 49.59	156 – 356.4	25
Orifice length	84.4 \pm 7.7	71.7 – 98.6	25
Orifice width	91.9 \pm 5.2	80.6 – 101.1	25
Ovicell length	192.4 \pm 34.6	130.6 – 257.5	13
Ovicell width	171.5 \pm 29.8	136.3 – 239.2	13
Avicularium length	72.3 \pm 6.7	60.5 – 78	7
Avicularium width	39.2 \pm 4	33 – 42.2	7

Remarks

Nine colonies of *Schizoporella errata* were found in Qatar coastal waters in station 7 encrusting on coral rubble and on a glass bottle. *Schizoporella errata* was first recorded in Qatar by Al-Ansi and Al- Khayat (1999) in Halul island , followed by Al-Khayat and Al-Maslamani (2001) who reported that *Schizoporella errata* is an important fouling organism, because its colony formed broad laminar encrustation on pearl oyster shells *Pinctada radiata* shell which was only found in one station, (Hallah Dalmma, station 5).

Schizoporella errata are a widespread warm temperate subtropical species. Originally described from Naples, Italy, it is found throughout the Mediterranean, West Africa, eastern Canada, eastern coasts of the Americas, from North Carolina through the Caribbean to Brazil, Pacific coast of North America, Red Sea, Arabian Gulf, South Australia, and New Zealand (Tilbrook et al., 2001). It is not surprising to find it in Qatar waters.

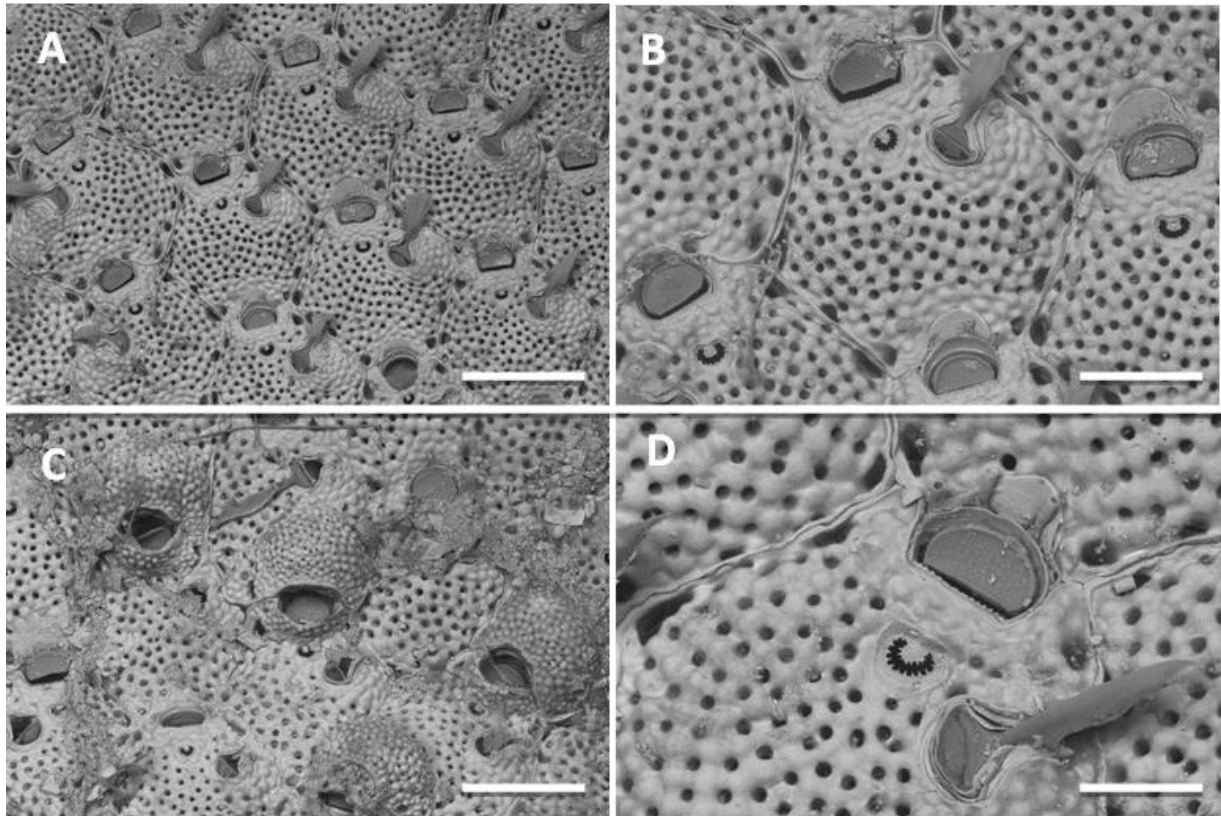


Figure 4.32: Scanning electron micrographs of *Microporella orientalis*, A: close-up of a group of zooids (scale bar= 100 µm), B: close-up of a group of zooids orifice, operculum, oral spines and ascopore (scale bar= 100 µm), C: close-up of an ovicellate group of zooids (scale bar= 100 µm), D: extra close-up of zooid orifice denticulate proximal edge, operculum, oral spines, ascopore and avicularium (scale bar= 20 µm).

Family *Microporellidae* Hincks, 1879

Genus *Microporella* Hincks, 1877

Microporella orientalis Harmer, 1957

Microporella orientalis – Harmer, 1957: p. 962, pl. 62, Figs 25–28, 38; Ristedt & Hilmer, 1985: p. 137, pl. 3, Fig. 3; Ryland & Hayward, 1992: p. 279, Fig 25 E, F; Tibbrook, Hayward and Gordon, 2001, p. 87, Fig. 19C, D.

Material

Qatar: QTR-MGR-00022, collected offshore at 14.2 m depth, found attached to coral rubble substrata (Appendix J).

Description:

The colony grows as an encrusting, orange, brown colour, unilaminar sheet. Autozooids have a D-shaped primary orifice, with a straight, finely denticulate proximal edge. Four distal oral spines are present. The frontal shield is nodular, densely perforated by small round pores. The ascopore has a slightly raised rim and coarsely denticulate, crescentic lumen. A single adventitious avicularium is present on each autozooid, proximolateral to ascopore; rostrum narrow and narrowest distally; mandible setiform or variably broadened, and with a pair of short, hooked, lateral process enclose to the base. The ovicell is spherical, nodular, perforated by pores; ovicellate autozooids develop a thick peristome rim distal to the ascopore, fused on each side with the ovicell (Tibbrook et al., 2001).

Table 4.24: Characteristics measurements of *Microporella orientalis* species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozooid length	338.2 \pm 29.1	267.1 – 383	21
Autozooid width	276.1 \pm 29	229.5 – 323.3	21
Orifice length	49.9 \pm 7.8	33.38 – 64.5	21
Orifice width	69.8 \pm 10.1	44.5 – 84	21
Ovicell length	133.7 \pm 16.6	115.3 – 159.5	7
Ovicell width	198 \pm 16	187.1 – 233	7
Avicularium length	71.3 \pm 12	48.1 – 96.9	21
Avicularium width	52 \pm 9.1	39.1 – 71.4	21
Ascopore length	26.8 \pm 6.6	16.2 – 41.5	21
Ascopore width	31.3 \pm 6.6	18.4 – 43.6	21
Mandible length	245.3 \pm 48.6	177.8 – 303.4	7
Mandible width	54 \pm 12.6	34.5 – 69.3	7

Remarks

Microporella orientalis from Qatar had four distal oral spines. *Microporella orientalis* described from Indonesia had three distal oral spines in early ontogeny, but spine number was not mention with respect to the adult zooids. In Qatar six colonies of this species were found

encrusting on coral rubble, one colony was recorded from station 1 and five colonies were recorded from station 9. *Microporella orientalis* was originally described from Indonesia, and recorded from the Great Barrier Reef by Ryland & Hayward (1992), who commented that this species occurs throughout the western Pacific and perhaps the Indian Ocean (Tibbrook et al., 2001).

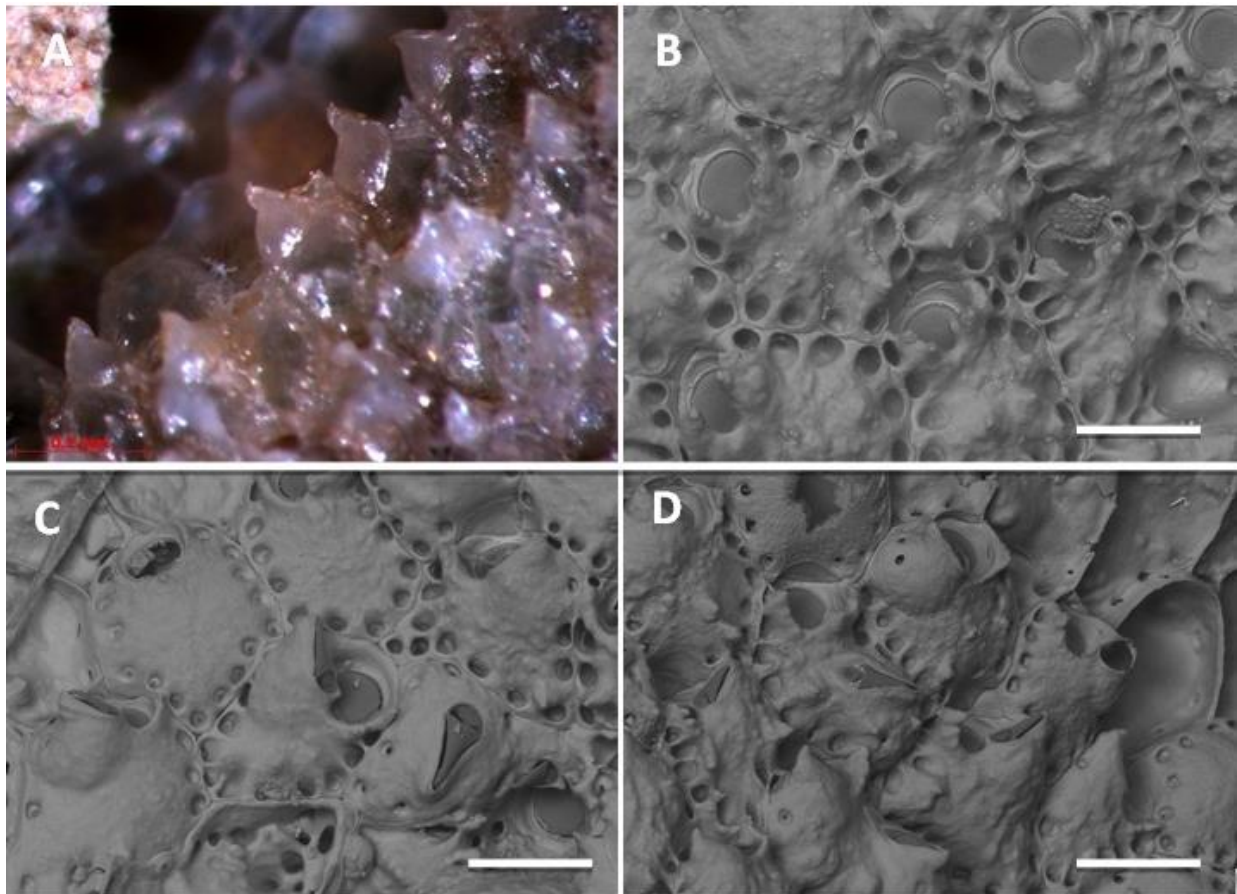


Figure 4.33: A: ZEISS microscope picture of *Rhynchozoon* sp. (scale bar= 0.2 mm), B: Scanning electron micrograph of group of zooids (scale bar= 100 μ m), C: close-up of a group of zooids orifice, operculum, marginal pores and avicularium (scale bar= 100 μ m), D: group of zooids at colony edge (scale bar= 100 μ m).

Family *Phidoloporidae* Gabb & Horn, 1862

Genus *Rhynchozoon* Hincks, 1895

Rhynchozoon sp.

Material

Qatar: QTR-MGR-00023, collected offshore at 14m depth, found on coral rubble substrata and on pear oyster shells *Pinctada radiata* (Appendix J).

Description

Colonies develop grey, domed multilaminar patches. Autozooids are oval to hexagonal, convex, with distinct boundaries marked by shallow grooves. The frontal shield is smooth, finely granular, with distinct marginal pores and one to two frontal umbones. The primary orifice is slightly wider than long, with U-shaped sinus and finely denticulate rim. No oral spines are present. The peristome is developed laterally and proximally; with three umbo, and incorporating a single lateral avicularium, on the right or left. The avicularium is cystid and rounded, the distal tip is frequently developed as a conspicuous spiked process; rostrum triangular, perpendicular to orifice. Other adventitious avicularia situated away from the orifice. Ovicells are unknown.

Table 4.25: Characteristics measurements of *Rhynchozoon* sp. species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	225.8 \pm 34.5	149.4 – 278.5	30
Autozoid width	184.5 \pm 49.1	115.8 – 393.95	30
Avicularium length	117.9 \pm 27	78.2 – 197.2	17
Avicularium width	80.1 \pm 17.6	36.9 – 103.7	17

Remarks

The shape of avicularia of *Rhynchozoon* species from Qatar differs from *Rhynchozoon* species from the Solomon Islands described by Tilbrook (2006) as well as species from Heron Island, Queensland, Australia described Ryland and Hayward (1992).

The primary orifice and the sinus in Qatar species was obscured and not fully clear to be measured. Thirty eight colonies of this species were found across the stations except in station 3. Station 7 had the highest number of colonies recorded (20 colonies) than the other stations. This species was found encrusting on coral rubble substrata and on pear oyster shells *Pinctada radiata*. *Rhynchozoon* species are common in tropical reef habitats world wide (Tilbrook, 2006).

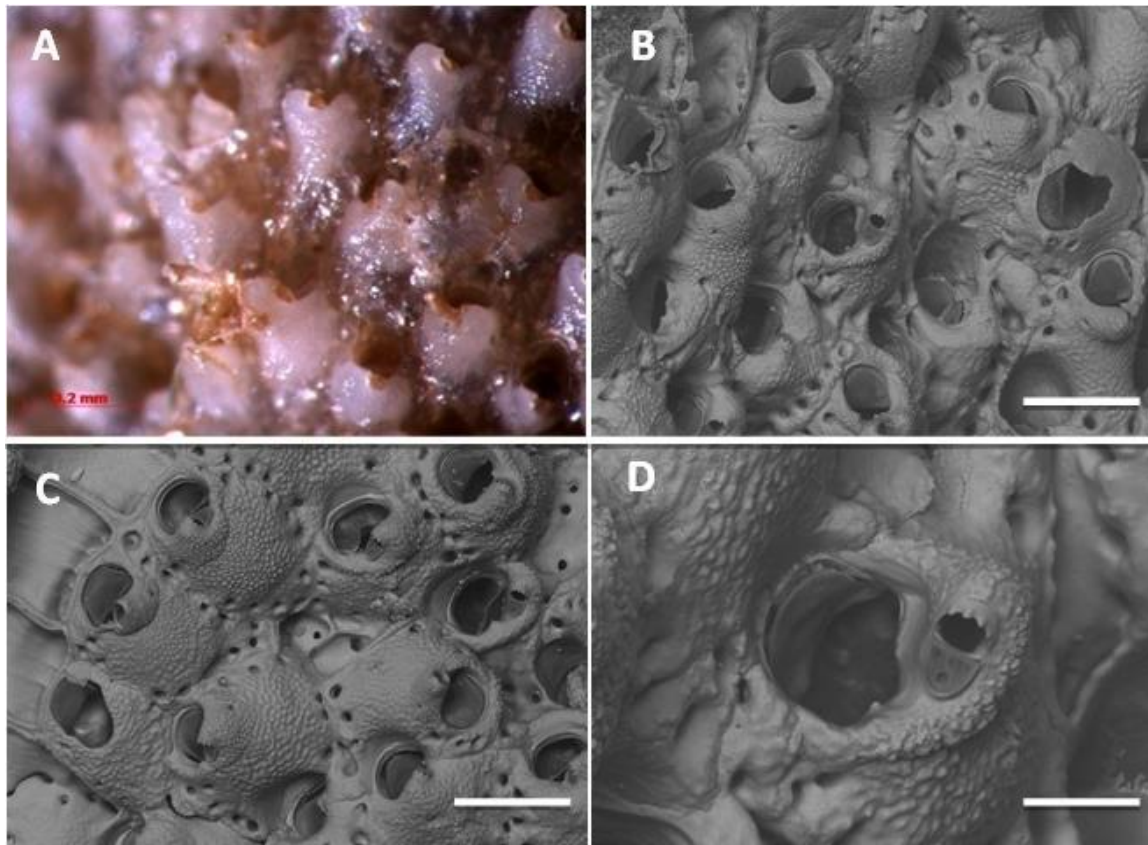


Figure 4.34: A: ZEISS microscope picture of *Celleporaria* sp.1 colony edge (scale bar= 0.2mm), B: scanning electron micrograph of *Celleporaria* sp.1 colony edge (scale bar= 200 µm), C: close-up of a group of zooids orifice, operculum, and avicularium at the base of the umbo (scale bar= 100 µm), D: close-up of zooids open orifice, U-shaped sinus and avicularium with toothed rim at the base of the umbo (scale bar= 20 µm).

Family *Lepraliellidae* Vigneaux, 1949

Genus *Celleporaria* Lamouroux, 1821

Celleporaria sp.1

Material

Qatar: QTR-MGR-00024, collected offshore at 14m depth, found on coral rubble substrata (Appendix J).

Description

The colony grows as encrusting, blue-green, forming multilaminar patches rising from the substrata. Autozooid are oval to hexagonal, convex, and separated by shallow grooves. The frontal shield is granular with large marginal pores. The primary orifice is orbicular, slightly wider than long, with a U-shaped sinus and small condyles. No oral spines are present. The

peristome is thick, enclosing the orifice proximally and laterally, developed proximally as a conical umbo, adjacent to a rounded pseudo-sinus. The avicularium is suboral, proximal, found at the base of the umbo. The distal rim of the avicularium is finely toothed. Ovicells were not seen.

Table 4.26: Characteristics measurements of *Celleporaria* sp.1 species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	271.91 \pm 37.8	208.1 – 350.3	19
Autozoid width	198.2 \pm 24.1	163.5 – 247.5	19
Orifice length	85 \pm 11.4	57.4 – 104.6	18
Orifice width	82 \pm 17.6	27.5 – 109.3	18
Avicularium length	67.3 \pm 9.9	56.3 – 85.1	6
Avicularium width	54.5 \pm 7.7	44.5 – 61.7	6
Mandible length	55 \pm 3.8	51.7 – 60	4
Mandible width	55.3 \pm 5.9	49.2 – 62.3	4

Remarks

Celleporaria sp.1 species from Qatar differs from *Celleporaria cylindrocystis* species from the Solomon Islands described by Tilbrook (2006) by the absence of lyrula. Qatar species also differs from *Celleporaria pigmentaria* from Heron Island, Queensland; Australia described Ryland and Hayward (1992) by the absence of vicarious avicularia.

Celleporaria species are distinguished by their primary orifice overall shape, the presence or absence of a proximal sinus and the shape of the suboral avicularium (Tilbrook, 2006). Seven colonies of this species were found in Qatar encrusting coral rubble substrata. Two colonies were found in station 1 and 5 colonies found in station 7. *Celleporaria* species have been described from the Indo-West Pacific, Southern Chinese seas, Mauritius, New Zealand and the Philippines (Tilbrook, 2006).

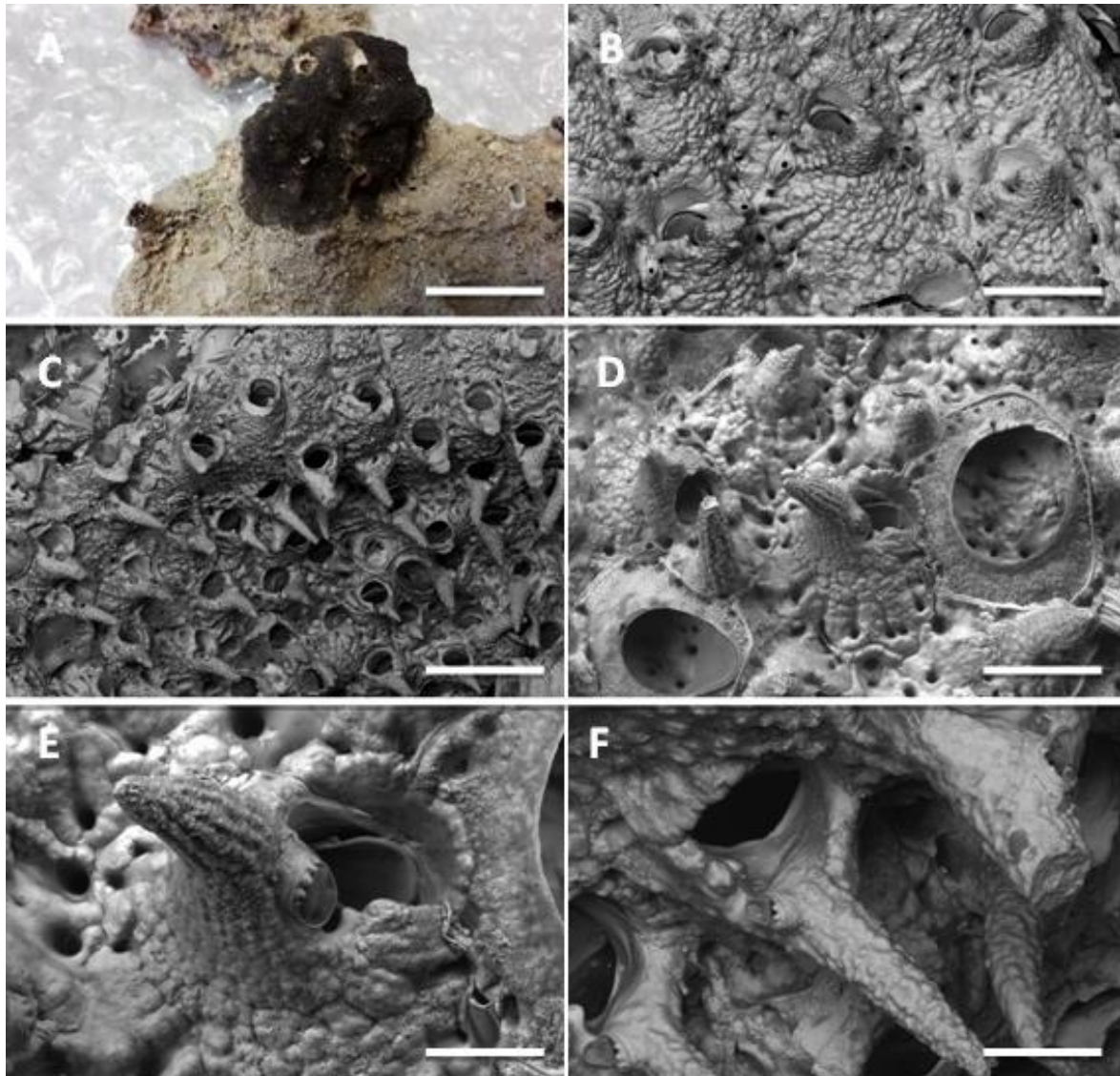


Figure 4.35: A: Picture of *Celleporaria* sp.2 encrusting coral rubble (scale bar= 2 cm), B: Scanning electron micrograph of *Celleporaria* sp.2 zooids at colony edge (scale bar= 200 µm), C: close-up of a group of zooids orifice and peristome with proximal conical umbo (scale bar= 100 µm), D: close-up of a group of zooids (scale bar= 100 µm), E, F: close-up of zooid open orifice, peristome with proximal conical umbo, and avicularium with toothed rim at the base of the umbo (scale bar= 20 µm).

Celleporaria sp.2

Material

Qatar: QTR-MGR-00025, collected offshore at 15m depth, found on coral rubble substrata and on pear oyster shells *Pinctada radiata* (Appendix J).

Description

The colony grows as an encrusting, black sheet with a few white spots visible to the naked eye. Autozooids are oval to hexagonal, convex, and separated by shallow grooves. The frontal shield is granular with large marginal pores. The primary orifice is orbicular, with a U-shaped sinus. No oral spines are present. The peristome is thick and deep, enclosing the orifice proximally and laterally, developed proximally as a conical umbo, adjacent to a rounded pseudo-sinus. The avicularium is suboral, proximal, at the base of the long spine. The distal rim of the avicularium is finely toothed. Other avicularia present are paired and lateral to the orifice; cystid small, not globular and mandible slender. Ovicells are unknown.

Table 4.27: Characteristics measurements of *Celleporaria* sp.2 species found in Qatar.

Measurements	Mean \pm SD (μm)	Range (μm)	Zooids Number
Autozoid length	178.6 \pm 38	131.9 – 279.2	26
Autozoid width	99.7 \pm 15.3	71.4 – 133.4	26
Orifice length	36.2 \pm 5.9	21.6 – 47.8	26
Orifice width	38.4 \pm 5.4	30.1 – 49	26
Spine length	70.7 \pm 21.3	46.4 – 114.4	21
Spine width	25.4 \pm 6.7	14.6 – 42.2	21

Remarks

The spine shape of *Celleporaria* sp.2 species from Qatar differs from *Celleporaria cristata* (Lamarck, 1816) and *Celleporaria columnaris* (Busk, 1881) from Australia in which the latter are characterized by multiple spines and huge spine respectively.

The most characteristic feature of this species is its black colour and the suboral avicularium situated proximally at the base of a huge umbo. Eight colonies of this species were recorded in Qatar; one colony from station 3 and 7, and six colonies from station 9. *Celleporaria* species can form large colonies in tropical and subtropical seas (Tilbrook, 2006).

4.4.3. Bryozoa species diversity analysis

Overall, one Ctenostome and 24 Cheilostome bryozoan, species were recorded from 168 samples across the East-North coastline of Qatar. Station 1 had the highest number of species (n =17). The site with the lowest number of species was station 3 (n = 4) these findings are summarised by site in Table 4.28.

Table 4.28: Presence of bryozoan species from Qatar at sampling stations.

Species	Station 1	Station 2	Station 3	Station 5	Station 7	Station 9
Phylum: Bryozoa						
Class: Gymnolaemata						
Order Ctenostomatida						
<i>Nolella</i> sp.				✓	✓	
Order: Cheilostomatida						
<i>Synnotum aegyptiacum</i>	✓					
<i>Aeta ligulata</i>	✓					✓
<i>Biflustra</i> sp.					✓	
<i>Parellisina</i> sp.	✓			✓		✓
<i>Akatopora</i> sp.		✓		✓		
<i>Smittipora harmeriana</i>	✓					
<i>Odontoporella</i> sp.	✓			✓		
<i>Predanophora longiuscula</i>						✓
<i>Caulibugula</i> sp.	✓					
<i>Puellina egretta</i>	✓					
<i>Poricella robusta</i>	✓					✓
<i>Drepanophora indica</i>	✓	✓		✓		
<i>Trypostega johnsoulei</i>	✓	✓	✓	✓	✓	✓
<i>Chorizopora brongniartii</i>					✓	
<i>Thalamoporella granulata</i>						✓
<i>Exechonella brasiliensis</i>	✓					✓
<i>Parasmittina raigii</i>	✓	✓	✓			
<i>Parasmittina egyptiaca</i>	✓		✓	✓	✓	✓
<i>Parasmittina spondylicola</i>	✓	✓		✓	✓	
<i>Schizoporella errata</i>					✓	
<i>Microporella orientalis</i>	✓					✓
<i>Rhynchozoon</i> sp.	✓	✓		✓	✓	✓
<i>Celleporaria</i> sp.1	✓				✓	
<i>Celleporaria</i> sp.2			✓		✓	✓

Station 1 had the highest number of species (S), total individuals (N) and epifaunal diversity (H [Loge]) than the other stations. Station 3 had the lowest numbers in all diversity indices. The epifaunal community in station 3 and 5 are less numerically equal than the other stations according to Pielou's evenness (Table 4.29).

Table 4.29: Means of S, N, d, J, H [Loge] and 1-Lamda from all stations.

Site	Total species (S)	Total individuals (N)	Species richness (d)	Pielou's evenness (J)	Shannon Wiener diversity (H[Loge])	Simpson's diversity (1-Lamda)
Station 1	17	97	3.4	0.7	2.2	0.8
Station 2	6	16	1.8	0.8	1.5	0.7
Station 3	4	34	0.8	0.5	0.8	0.4
Station 5	9	40	2.1	0.5	1.2	0.5
Station 7	10	83	2.0	0.7	1.6	0.7
Station 9	11	69	2.5	0.7	1.8	0.7

4.4.4. Bryozoa species mineralogy analysis

Results of the X-ray Diffraction analyses showed that most cheilostome bryozoans from Qatar have bimineralic skeletons with variation in Mg content; *Rhynchozoon* sp. had both low Mg-calcite (0–4 mol% MgCO₃) and high-Mg calcite of (>12 mol% MgCO₃). *Parasmittina egyptiaca*, *Trypostega johnsoulei* had high-Mg calcite. *Schizoporella errata*, *Poricella robusta*, *Thalamoporella granulata* and *Biflustra* sp. had intermediate Mg-calcite (4–12mol% MgCO₃) (Smith et al., 2006; Taylor et al., 2014). *Thalamoporella granulata* and *Biflustra* sp. had calcitic skeletons. Both *Celleporaria* species had aragonitic skeleton (Table 4.30, Figure 4.36).

Table 4.30: Results of the high precision Nonius X-ray Diffractometer analyses of Qatar cheilostome bryozoans.

Species	Family	Locality	Mineralogy	Mg content	No. Of replicates
<i>Biflustra</i> sp.	<i>Membraniporidae</i>	Station 7	Calcitic	Intermediate	3
<i>Trypostega johnsoulei</i>	<i>Trypostegidae</i>	Station 7	Bimineralic	High	3
<i>Parasmittina egyptiaca</i>	<i>Smittinidae</i>	Station 7	Bimineralic	High	3
<i>Schizoporella errata</i>	<i>Schizoporellidae</i>	Station 7	Bimineralic	Intermediate	3
<i>Poricella robusta</i>	<i>Arachnopusiidae</i>	Station 9	Bimineralic	Intermediate	3
<i>Thalamoporella granulata</i>	<i>Thalamoporellidae</i>	Station 9	Calcitic	Intermediate	3
<i>Celleporaria</i> sp.1	<i>Lepraliellidae</i>	Station 7	Aragonitic	-	1
<i>Celleporaria</i> sp.2	<i>Lepraliellidae</i>	Station 7	Aragonitic	-	1
<i>Rhynchozoon</i> sp.	<i>Phidoloporidae</i>	Station 7	Bimineralic	High & Low	3

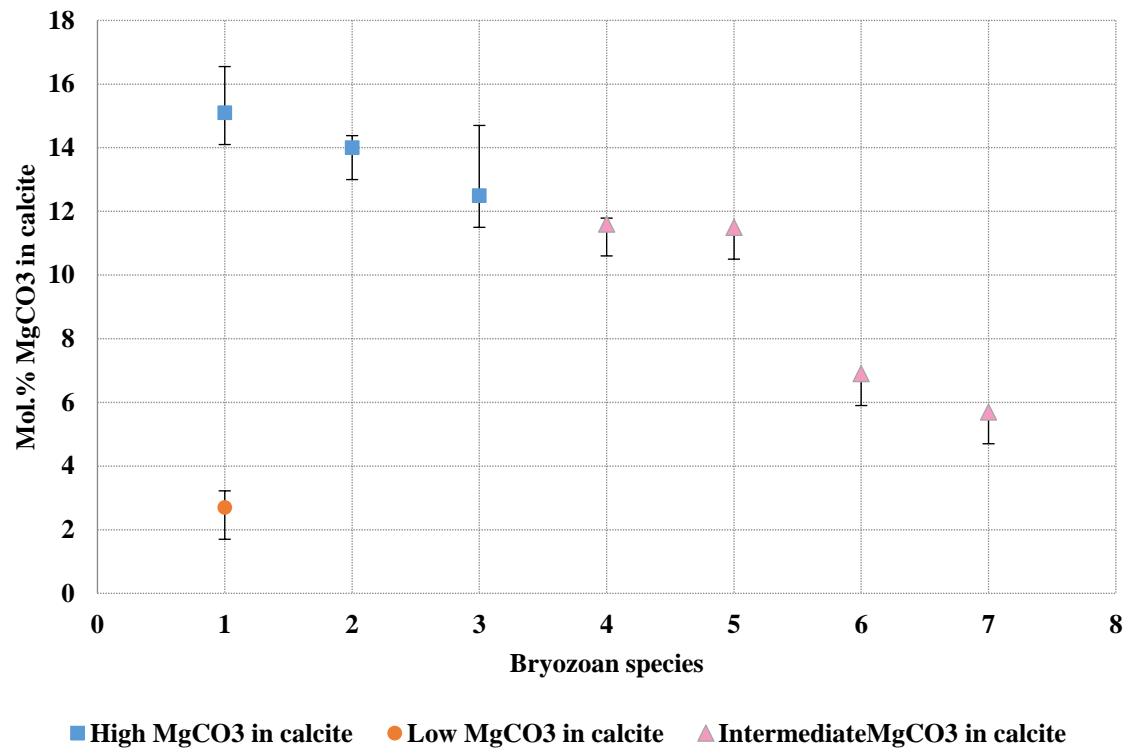


Figure 4.36: Qatari bryozoan species Mol. % MgCO₃ in calcite (1: *Rhynchozoon* sp., 2: *Trypostega johnsoulei*, 3: *Parasmittina egyptiaca*, 4: *Schizoporella errata*, 5: *Poricella robusta*, 6: *Thalamoporella granulata*, 7: *Biflustra* sp.).

4.5. Discussion

The overall aim of this chapter is to document the biodiversity and skeletal mineralogy of Bryozoa from coastal waters of Qatar.

4.5.1. Diversity of Qatar Bryozoa

This first account of the cheilostome Bryozoa of Qatar included 25 species, 9 of which were new to science. This proportion of previously un-described species is not unusual for taxonomic and faunistic studies of the Arabian Gulf bryozoans, and it is certain that the total number of species recorded does not accurately represent the true taxonomic diversity of the cheilostomatida of Qatar, and further sampling at other localities and in other habitats, is needed before it can be reasonably estimated. The sample collections in this study were made during three days, at six locations of the ten on the East-North coastline of Qatar peninsula; the rest of the stations were unsampled. Collecting was conducted by SCUBA and the habitats sampled varied in live coral cover but had occasional gorgonians soft corals, common juvenile oysters, and fish burrows, and the substrata were coral rubble, shells, hydroids, sea fan, and sand dollar. Station 1 had the highest number of species, total colonies and epifaunal diversity than the other stations. The recorded average water temperature and salinity during the collection time were 30.1°C and 39.8 PSU respectively with minimum recorded variations across all stations. Further analysis is needed as well as the collections of more specimens from other stations to investigate the physiological and ecological factors such as respiration, growth, and feeding rates influencing the diversity in this station. The number of new Bryozoa taxa recorded reflects the previous lack of attention for sessile invertebrates, other than corals, that has been conducted by taxonomic specialists in Qatar. Environmental studies centre at Qatar University owns unpublished reports of bryozoan species (*Schizoporella cf. unicornis* and *Amphiblestrum* sp.) found in marine sediment samples from north of Raslaffan (Alrkiat, 2010).

4.5.2. Remarks on autozooid size variation and temperature

In this study, autozooids of *Chorizopora brongniartii* species from Qatar were smaller in size; measuring within a range of 103.2 – 232 µm in length and 81.2 – 147 µm in width, than autozooids of *Chorizopora brongniartii* from Ramsey Bay, Isle of Man; measuring within a range of 190.2 – 308.2 µm in length and 115.9 – 238.4 µm in width, as shown in Figure 4.37. These findings are in accordance with a study by Lombardi et al. (2006) that reported

bryozoan species can show morphological responses to environmental changes which may act on genotypic, phenotypic and eco-phenotypic levels, which explains the demonstration of autozooids size as a function of surrounding water temperature; cheilostome bryozoans produce large zooids in cool water while, smaller zooids are produced in warm waters. This occurs within species over geographical ranges and over seasonally derived changes in temperature and laboratory culture. A decrease in body size at higher temperatures was observed in many taxa and termed the temperature-size rule (O'Dea and Okamura, 2000; Lombardi et al., 2006).

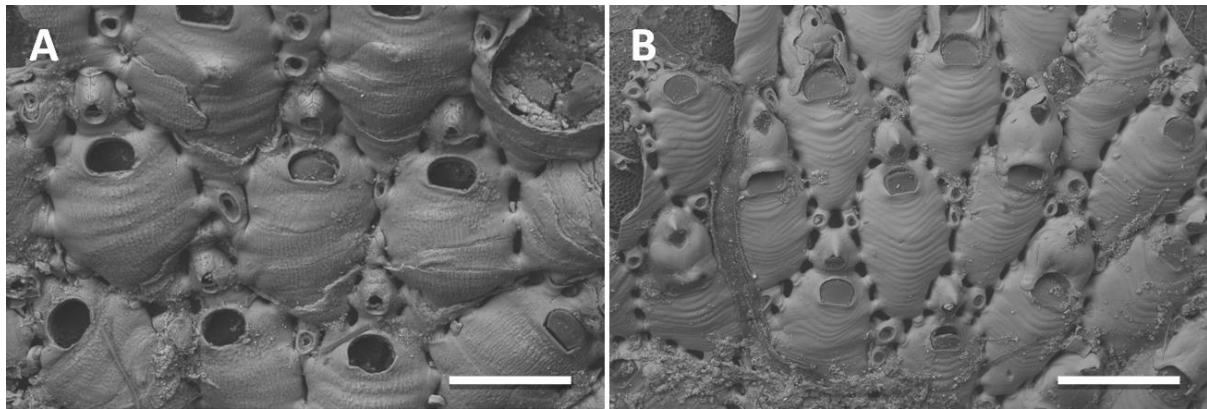


Figure 4.37: Scanning electron micrographs of *Chorizopora brongniartii*. A: a group of autozooids of *Chorizopora brongniartii* from Ramsey Bay, Isle of Man (scale bar= 100 µm), B: a group of autozooids of *Chorizopora brongniartii* from Qatar (scale bar= 100 µm).

A study by O'Dea et al. (2007) in the Gulf of Panama investigated if the fluctuations in temperature that occur during rising of the level of seawater could be responsible for the changes in bryozoan *Cupuladria exfragminis* zooid size by laboratory culturing under controlled temperatures. The study reported that the new budded zooids size in *Cupuladria exfragminis* colonies was significantly larger during times of low surrounding water temperatures and with the increase of temperature the colonies returned to produce smaller zooids. Therefore, as a colony buds new zooids along the margin; zooids respond accordingly to changes in seasonal temperatures.

In agreement with the above studies (O'Dea and Okamura, 2000; Lombardi et al., 2006; O'Dea et al., 2007), Amui-Vedel et al. (2007) also reported that in cultured colonies of *Cryptosula pallasiana*, zooids varied in length and width when exposed to different temperatures and were longer and wider at lower temperatures.

4.5.3. Remarks on the mineralogy of Qatar Bryozoa

Assessment of the vulnerability of Bryozoa to extreme ocean climate is complicated and skeletal mineralogies of different species must be taken into account. The first analysis of nine cheilostome bryozoan species from Qatar showed that most of them had bimineralic skeletons; two species were calcitic, two aragonitic and five bimineralic. Four bimineralic bryozoan species; *Parasmittina egyptiaca*, *Trypostega johnsoulei*, *Rhynchozoon* sp. and *Poricella robusta* were abundant and dominant represented by 242 colonies recorded from all stations. Due to the low number of Qatar bryozoan species analysed for mineralogy, the results previously mentioned in Section 4.4.4 can be seen as a starting point for understanding the mineralogy of the Qatar bryozoan fauna overall. Further studies might include investigating the Bryozoa of the west side of the Qatar peninsula in comparison to the eastern side as well as comparing the Qatar Bryozoa fauna mineralogy with patterns of mineralogy from other tropical faunas since there is few studies providing this type of data at the present time.

A study by Taylor et al. (2016) investigated the mineralogies of 22 species of cheilostomes of a tropical bryozoan biota, from Malaysia. During sampling, recorded temperatures were within the following range (29.7 - 32.3°C) which was closely similar to Qatar temperatures (Appendix Q). However, recorded salinities were lower than Qatar (27 - 33 PSU). The study examined the context of latitudinal increase in aragonitic bryozoans towards the equator as well as to contrast the mineralogy of a tropical biota with biotas from higher latitudes and reported that tropical cheilostome biota were rich in bimineralic and aragonitic species; 10 species were calcitic, six aragonitic and seven bimineralic. The study also reported there is a strong increase in aragonitic species towards the equator and a decrease in calcitic species due to latitudinal changes in the mineralogies of widely distributed genera. For example, species of the genus *Parasmittina* analysed from Malaysia were found to have aragonitic skeletons, whereas previous analyses of fossil species of this genus from higher latitudes showed them to be calcitic or bimineralic (Taylor et al. 2009). The precipitation of minerals in bryozoan cheilostomes skeletons might be influenced by environmental factors such as seawater temperature and chemistry (Lombardi et al., 2008)

In this study calcitic and bimineralic cheilostome Bryozoa in Qatar showed a wide range of variations in Mg-calcite content. The following species; *Rhynchozoon* sp., *Trypostega johnsoulei* and *Parasmittina egyptiaca* had high-Mg calcite (>12 mol% MgCO₃); 15.1 mol %

Mg, 14 mol % Mg, and 12.5 mol % Mg respectively. The Arabian Gulf is characterised by high seawater temperatures and in that environment, the smaller cation Mg^{2+} replaces Ca^{2+} in the calcium carbonate lattice leading to the formation of Mg-calcite MgCO_3 which is a harder material than CaCO_3 , but is thermodynamically unstable (Loxton et al., 2014). However, several studies reported that the MgCO_3 contents of cheilostomes whether calcitic or bimineralic rarely exceed 12 mole% (Lombardi et al., 2008; Taylor et al., 2009). The high-Mg calcite content in Qatar cheilostome species might suggest that the bryozoans are capable of demonstrating high metabolic activity as a survival mechanism to extreme environmental conditions.

In this study, x-ray diffraction analyses showed that *Celleporaria* sp.1 and *Celleporaria* sp.2 had aragonitic skeleton. Aragonite is more soluble than calcite in seawater and more vulnerable to ocean warming and acidification, however, acid-bath immersion experiments on bimineralic bryozoans failed to show the expected dissolution of the skeletons of bryozoan species containing aragonite (Smith, 2014; Taylor et al., 2016). Bimineralic zooid forms a box of calcite then adds a separate secondary coating of aragonite, generally on the frontal wall (Smith and Girvan, 2010). In ocean acidification, the surface area of the complex skeletons determines the dissolution rate of secondary aragonite and it varies with water temperature (Smith, 2014; Taylor et al., 2016; Smith and Girvan, 2010).

In this study, a total of 337 colonies of Qatar Bryozoa were recorded and upon examination there was no presence of dissolution or corrosion on the frontal walls. These species seem to endure extreme seawater temperatures and salinity of the Arabian Gulf. Conversely, a study by Rodolfo-Metalpa et al. (2009) on the effects of in situ exposure to low pH and high seawater temperature conditions on the calcification of calcitic skeleton of the Mediterranean *Myriapora truncata* Bryozoa showed that adult *M. truncata* colonies were resilient to acidification in seawater temperatures ranging from 19 to 24°C and intermediate pH (7.66 ± 0.22), however in elevated temperatures 25 to 28 °C and low pH (7.43 ± 0.31) calcification rates decreased to zero in *M. truncata*, as well as in *Stylophora pistillata* coral species, and killed the Mediterranean coralline alga *Lithophyllum cabiochae*. The study concluded that high seawater temperatures caused stress to these species and disabled their calcification.

Lombardi et al. (2011) suggested that the cuticle might protect the bryozoan skeletons against corrosion caused by the low pH of seawater. The study investigated the effects of acidification on *Myriapora truncata* growth and organic tissue composition. Living colonies

were exposed to different CO₂ vents and pH conditions. The study reported that in normal pH, seawater temperatures ranging between (25.1°C - 27.7°C) had no affect on colony growth. However, in low and intermediate pH environment the cuticle of *Myriapora truncata* increased in thickness which might suggest a protective mechanism against the dissolution of Mg calcite skeleton and the reallocation of energy functions to cuticle formation.

A knowledge gap exists between the involvement of physiological factors such as metabolism, life stages, growth rate and cuticular material thickness on the ability of Qatar Bryozoa to endure extreme Gulf climate. Such information in future studies may enable us to predict which species will survive and how the composition of assemblages will change in future environmental conditions.

5. Chapter 5: General discussion

5.1. Study findings

The overall aim of this study was to investigate the factors influencing biodiversity, abundance, spatial distribution and successional patterns of encrusting epifaunal communities in temperate and tropical biogenic habitats.

5.1.1. North- East Atlantic

This study reports that the following factors influenced the epifaunal communities encrusting *Modiolus modiolus* horse mussels:

1. Settlement position on the horse mussel shell; epifaunal species numbers and diversity were higher in the posterior region of the shell.
2. Horse mussel shell size; polychaetes and barnacle numbers were high in the medium and large shells. However, bryozoan abundance was high in small shells.
3. Bryozoan competition; bryozoan species competition was mainly on the posterior region of the horse mussel shells and dominated by standoff interaction. Competition between bryozoans was higher in small shells than larger ones.

5.1.2. Arabian Gulf, Qatar

This study reports the first description of cheilostome Bryozoa from Qatar and included 25 species, nine of which were new to science. The study also reports the first measurements of the skeletal mineralogy of Qatar Bryozoa. Sufficient material was available from nine species to analyse. The majority of these had bimineralic skeletons with a wide range of variations in Mg-calcite content.

5.2. The importance of *Modiolus modiolus* mussel habitats

Modiolus modiolus mussel beds have ecological significance for the marine environment due to their highly complex structures on the seabed which increases the availability of food and substrata for larvae settlement as well as provide refuge from predators and physical unfavourable disturbances (Rees, 2009; Sueiro et al., 2011). Communities associated with *M. modiolus* beds are diverse, with a wide range of epibiota and infauna including hydroids, barnacles, polychaete, red seaweeds, solitary ascidians and bryozoans (Rees, 2009).

While there are as yet no studies on the epifaunal communities associated with *Modiolus modiolus* horse mussel reef habitat, studies have been conducted on various other shellfish

species. Sueiro et al. (2011) investigated the relationship between increasing habitat complexity and the diversity of sessile invertebrate assemblage when associated with three different ecosystem habitats; *Spartina densiflora* cord-grass, dense beds of the mussels *Perumytilus purpuratus* and *Brachidontes rodriguezii*, and the barnacle *Balanus glandula* dominated habitat. The study reported that both of the complex habitats cord-grass and mussels were more species rich and diverse than the barnacle habitat. Sueiro et al. (2011) reported that greater habitat structure and physical dimensions of the cord grass increased the availability of surface for species colonization relative to that of the barnacle.

The current study shows that the epifaunal communities diversity supported by the horse mussel shell surface, contributes highly to the biodiversity of the whole reef system. A total of 400 horse mussels have been analysed from Skarnsundet West Bridge, Norway in the North to Llŷn Peninsula in the South and 54 epifaunal species were seen to colonise the shells of horse mussels showing that horse mussels are able to support high levels of epifaunal biodiversity.

5.3. Epifaunal communities in a temperate water context: North-East Atlantic

In this study, total epifaunal species abundance and diversity in all sites were higher in the posterior region of the horse mussel shells (Section 2.4.7) due to the action of horse mussel filter feeding through the inhalant and exhalant siphons that are found within the posterior region of the shell (Dinesen and Morton, 2014). The size selective feeding behaviour by mussels affects the marine ecosystem via filtration of particles, and the release of biodeposits including faeces and pseudofaeces (Warwick, 1997; Jansen et al., 2011). Partitioning of food resources depends on the physical factor of mouth size which influences the structure of encrusting epifaunal communities (Taylor, 1979).

In this study the epifaunal communities were similar in some sites of the North-East Atlantic, except in Loch Creran and Dornoch Firth which had the largest shell size and the epifaunal communities were different due to the low abundance of bryozoans. SIMPER analysis previously described in chapter 2 (Table 2.10) showed that in all sites shell epifauna were dominated by the polychaete worm *Spirobranchus triqueter*, the barnacle *Balanus balanus*, and the ubiquitous bryozoan *Escharella immersa*. Arribas et al. (2013) reported that similarities and differences in epifaunal communities between different sites are greatly influenced by physical factors of the habitat and interactions between organisms leading to spatial variation.

Koivisto et al. (2011) investigated epifaunal diversity and taxonomic composition in three different densities in *Mytilus edulis* blue mussel beds. Bed (I) contained small mussels with a sparse density of large mussels, bed (II) contained mixed sized mussels and intermediate density of mussel and bed (III) contained mixed sized mussels with a high density of large mussels. The study reported that the highest epifaunal species diversity and abundance was in bed (II). In early succession stage in bed (I), opportunistic species such as gastropods, clams and crustaceans were frequent in the increased surface area and with further stages of succession polychaetes, flatworms and priapulid worms which were absent in bed (I) became dominant in bed (III) due to the increase of organic matter trapped between the mussel shells. This might indicate that big-sized blue mussels are favourable for certain epifaunal species and different densities and sizes of mussel are associated with different epifaunal taxonomic groups. Conversely a study by Commiato et al. (2008) investigated *Mytilus edulis* mussel beds and associated epifauna on three different sediment sites (gravel, sand, mud) in Maine, USA using distance-based per-mutational multivariable analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity measures. Fifty nine epifaunal species were recorded from the three sites and polychaetes were the most dominant species. Non-metric multi-dimensional scaling (nMDS) showed no differences in the epifaunal communities between the sites which could be due to the presence of mussels in the mud site which provided hard substrate for epifaunal species attachment and refuge. The study also reported that in mussel beds, the low abundances of certain species may be due to predation rather than altered environmental conditions.

In this study, results of shell size analysis showed significant correlations between shell size and species abundance. Polychaetes and barnacle numbers were highest in the medium and large shell size class. However, bryozoan abundance and competition was higher in small shell size classes that decreased with the increase of shell size as previously mentioned (chapter 2, Figure 2.15; chapter 3, section 3.4.4). A proposed hypothesis would be predation on mussels either by ingestion or damaging the shell by feeding associated activities plays a role in the absence of bryozoans in larger shells and affects community structure and diversity. Further future studies are needed in order to test this hypothesis. To our knowledge there is no published research on the effects of predation on *Modiolus modiolus* horse mussels but there are various studies regarding other species of mussels. A study by Enderlein and Wahl (2004) investigated the affects of predation of shore crab *Carcinus maenas*, the common starfish *Asterias rubens* and the periwinkle *Littorina littorea* on the

dominance of *Mytilus edulis* blue mussel in situ experiments carried out in the Tonnenhof, Kiel Fjord, Baltic Sea. Shore crabs feed on mussels up to 50 mm of shell length, while starfish prey on mussels up to 33 mm in length and periwinkles ingest and damage new settled organisms. In the environment prior to introducing the three predators, the number of blue mussel was increasing and accompanied by a rising diversity of associated epifauna. With time the dominance of *Mytilus edulis* was accompanied by a decrease in associated epifauna and the disappearance of certain bryozoan species such as *Conopeum*. This was explained as a result of intense competition between epifaunal species during low stress and low predation conditions. On the other hand after the introduction of shore crabs, starfish and periwinkles the number of blue mussel decreased with the establishment of different associated epifauna such as barnacles and algae. The study reported that the presence of barnacles which create a rigid surface on the shells decreased the efficiency of periwinkles grazing. On the other hand the abundance of barnacles was decreased by the presence of starfish and shore crab.

Observations related epifaunal species (bryozoans, polychaetes and barnacles) dominance in different shell sizes and the above study might be explained by the following hypothesis in which dominance of polychaetes and barnacles on large shells, could be due to their high calcification, morphological features such as size and aggregative behaviour which protect them from predation to a degree (Jackson, 1977). Also, predation pressure and intense inter-specific competition for space by bryozoans may lead to mortality on large shells. A study by Perry et al. (1997) investigated the effects of predation by crayfish *Orconectes rusticus* on population density and size structure of Zebra mussels *Dreissena polymorpha* using cage experiment. Before the introduction of crayfish, Zebra mussels were uniformly distributed on the artificial cobble. Introduction of crayfish caused a reduction in the number of zebra mussels and lead the remaining Zebra mussels to occupy the inter-cobble spaces which provide spatial refuge from predation. The study predicted that only small sized zebra mussels would be consumed by crayfish however, Zebra mussels of all sizes were consumed with larger shells being more vulnerable. This finding was further explained by Djuricic, and Janssen (2001), who conducted field experiment on types of Zebra mussel refuge from round goby predation. The bottom of rocks can provide shelter but with a disadvantage for larger shells; small space, reduced food and slow growth. The clusters of Zebra mussel and their individual positions within the cluster also provide a refuge; the presences of small shells between larger ones make them hard to be removed by predators.

Behavioural responses in mussels such as clumping protect mussels against environmental stress and predators (Khalaman and Lezin, 2015). In this study intensive clumping was observed in the Noss Head site which had the highest level of diversity (Table 2.11), the greatest proportion of smaller shells (Figure 2.14), and had the highest number of bryozoan competitive interactions (section 3.4.2). These findings indicate that mussel beds might regulate the diversity of epifaunal species. Horse mussel bed habitats with their associated epifaunal communities are vulnerable to fisheries activities and would benefit by being included in a protected management framework (Boulcott, et al., 2014). Future studies might include investigating the effect of environmental factors such as sediment accumulation, current flow and temperature as well as disturbance on the diversity of epifaunal communities encrusting horse mussels.

5.4. Competitive interaction between bryozoan species

Competition for space and food has an important influence on the structure and diversity of marine hard substratum communities (Barnes and Rothery, 1996). In total 847 competition interactions were recorded between bryozoan species encrusting horse mussel shells across the North-East Atlantic. The results of this study showed that bryozoan competition is largely found on the posterior region of the horse mussel shells and the assemblage was dominated by standoff interaction between bryozoan species; in order to avoid mortality from overgrowth. Taylor (1979) reported that bryozoans possess three different strategies for competition of substrate. First strategy is to avoid overgrowth by developing erect growth above the substrata to disperse zooids over a wide area. Also during larva selection of substrate a preferred settlement would be away from strong competitors. Second strategy is overgrowth by fast growing species against competitors. Third strategy is defensive morphological characteristics such as the development of spines, peristome and raised borders on colony edges to avoid overgrowth. Also bryozoan species resist fouling by multilaminar growth by budding new zooids over pre-existing ones onto the surface of the colony to overgrow any settled organisms on its surface. Overgrowth competition between bryozoan species on artificial panels was further investigated by Gappa (1989) and reported that among the following four *Celleporella* species; *Celleporella hyalina*, *Celleporella yagana*, *Celleporella patagonica* and *Celleporella bougainvillea*, *Celleporella hyalina* was the strongest competitor due to its natural defensive strategy of multilaminar growth even in the absence of competitors. On the other hand, the remaining *Celleporella* species were abundant but weak competitors with a short life cycle due to their ability to reach early sexual

maturity and the production of high numbers of ovicells as a mean to avoid overgrowth by competitors. In epifaunal communities, the following factors such as; morphological characteristics, colony shape (erect or encrusting sheet) and rate of growth determine the outcome of bryozoan species competition for space. Asch and Collie (2008) reported that bryozoans encrusting growth form, fast growth rates and short life span (10 days - 1 year) provide a competitive advantage after disturbance in their environment by the ability to repair structural damage. Future work could include investigating the effects of environmental conditions such as resource stress, predation stress and disturbance on the outcomes of bryozoan competitive interactions in the marine environment.

5.5. Bryozoa communities in a tropical water context: Qatar

Bryozoans are important carbonate producers and play an important role in the ocean carbon cycle. Bryozoan skeletons are complex structures made of calcite and aragonite together with varying amounts of magnesium and are affected by existing and variation levels of ocean acidification which makes them an important subject of research in climate change as there is a positive correlation between mol% $MgCO_3$ in calcite in bryozoan skeleton and environmental temperature (Loxton et al., 2014; Fortunato, 2015). Increase in ocean temperatures can result in strong selection for the more tolerant bryozoan species and reorganizations at the ecosystem level that could have implications for the diversity and functioning of communities (Taylor et al., 2014).

The present study provides the first taxonomic information about the encrusting bryozoan fauna associated with coral reefs and pearl oyster *Pinctada radiata* along the East-North coastline of Qatar. Twenty five species were recorded and nine of them are new species. The first skeletal mineralogy analysis of nine Qatar cheilostome taxa showed that most were bimineralic with a wide range of variations in Mg-calcite content. Examination of bryozoan specimens showed no evidence of dissolution or corrosion on the frontal walls; this may indicate Qatar bryozoan species seem able to tolerate the combination of extreme seawater temperatures and high salinity of the Arabian Gulf. Sorte et al. (2011) investigated the variation in thermal tolerances of tunicates *Diplosoma listerianum* and the bryozoan *Bugula neritina* in the United States between the east with 26.4°C water temperature and the west coast with 24.4°C water temperature and reported that tunicates and bryozoans examined along the east coast of the United States had higher tolerances to temperatures than populations along the west coast. The study reported that marine species sensitivity to climate

change is determined by factors such as physiological limits, ecological traits, genetic diversity, adaptation and life history that will have an important role in the response of marine species to increasing seawater temperatures. A study by Burrows et al. (2014) emphasized the importance of changes in climate conditions on predicting future species distributions and persistence and the implementation of effective conservation strategies. The study also predicted that marine habitats rich in species might face a decline in their population due to the increase in sea water temperatures causing species to migrate to other areas with favourable climate leaving no replacement and causing local extinction events.

5.6. Future studies in Qatar

Bryozoan species in Qatar represent an important opportunity for research and future studies. It would be useful to consider using the naturally extreme ecosystem conditions of the Arabian Gulf as a model for future climate change in the region, and to compare with other areas. Topics to follow up for investigation include community structure, population dynamics, life history, and other aspects of Qatar Bryozoa ecology. Future studies might include documenting the effect of seawater temperature, salinity and food availability on colony growth rate and mineralisation in Qatar Bryozoa using artificial panels deployed in different sites along the coastline of Qatar. The Arabian Gulf also provides an opportunity to study molecular and physiological mechanisms of bryozoans that allow them to persist in this extreme environment, and explore whether these mechanisms might be shifted to other regions via the migration of species. Current studies are mainly focussed on the impacts of climate change in cold water and in temperate water environments. There are few studies on the impacts of climate change in recent tropical bryozoan faunas and in extreme high temperature and high salinity environments, and so this area has the potential to be explored for further studies.

5.7. Biogenic reefs and epifauna in temperate versus tropical environments

Further research in Qatar waters might lead to future comparison between temperate and tropical biogenic reef environments across the regions. Such as; diversity of the *Modiolus* shells study could be repeated using Pearl Oysters to establish whether the same factors driving the patterns of the epifauna distribution on the *Modiolus* are similar or different to what is driving the biodiversity patterns on the Oyster reefs. Having the knowledge regarding the succession patterns of the epifauna on the Oyster reefs may be of interest in relation to understanding successful restoration for the Pearl Oysters. A study by Cook (2016)

investigated which potential substrate could be used in the restoration of *Modiolus modiolus* reef. The study used different treatments; oyster cultivation bags filled with whole dead scallop shells, oyster cultivation bags filled with crushed scallop shells and oyster cultivation bags filled with concrete pieces. In collaboration with the Natural History Museum London, a V-Factor citizen science project was designed to analyse in detail the epifauna which colonised the whole dead scallop shells after deployment on site in Scapa Flow, Loch Creran and North Llŷn. After one year of deployment, the whole dead scallop shells were encrusted with colonies of Bryozoa, as first settlers. Interestingly, species of Cyclostome Bryozoa such as *Plagioecia* were dominant on the shells (Figure 5.1).

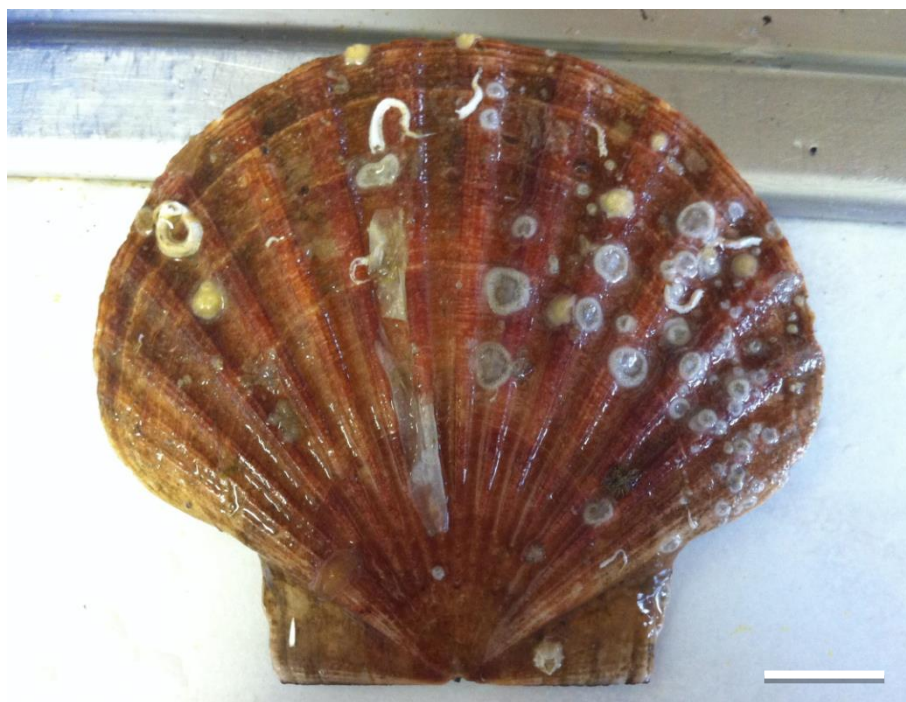


Figure 5.1: Scallop shell encrusted with *Plagioecia* bryozoan species from Scapa Flow, Orkney (scale bar = 8 cm).

This information is not yet published in an academic journal but supports other published information indicating that Bryozoa may be important in the mollusc reef biogenic habitats in the early stages of succession (Asch and Collie, 2008). This kind of information is important, when understanding colonisation patterns as a part of restoration protocols for the recovery of damaged reefs. Further studies are needed to investigate if patterns of colonisation would be similar if restoration projects were applied in Qatar waters to retrieve pearl oysters areas that have been impacted by physical disturbances.

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Appendices

Appendix A. North-East Atlantic horse mussel shell measurements

Ramsey Bay, Isle of Man

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
IOM 1	100	36	48	51.6
IOM 2	110	45	50	56.8
IOM 3	112	45	54	58.8
IOM 4	113	44	56	59.2
IOM 5	90	35	43	46.9
IOM 6	91	37	49	59.5
IOM 7	110	47	54	57.5
IOM 8	106	41	49	56.5
IOM 9	112	46	52	60.1
IOM 10	101	44	51	52.9
IOM 11	108	44	50	57.4
IOM 12	93	37	46	50.4
IOM 13	97	43	48	51.6
IOM 14	100	42	52	50
IOM 15	118	49	55	63.6
IOM 16	86	39	39	46.3
IOM 17	108	45	54	58.3
IOM 18	94	39	43	49.1
IOM 19	105	42	50	53.3
IOM 20	107	42	53	55.5
IOM 21	99	40	56	51.6
IOM 22	117	47	55	60.1
IOM 23	94	39	50	48.6
IOM 24	102	40	50	53.2
IOM 25	93	38	49	49.4
IOM 26	107	44	50	56.6
IOM 27	108	45	50	57.4
IOM 28	102	36	51	51.6
IOM 29	106	40	53	55.5
IOM 30	109	41	54	57.5
IOM 31	119	49	56	62.5
IOM 32	97	43	50	49.8
IOM 33	114	48	52	58.8
IOM 34	101	46	48	52.9
IOM 35	103	40	50	53.7
IOM 36	104	48	50	54.8
IOM 37	105	40	50	52.6
IOM 38	97	34	50	49.2
IOM 39	109	44	50	53.5
IOM 40	122	50	55	61.2
IOM 41	103	44	60	57.8
IOM 42	119	47	57	62.4
IOM 43	117	45	55	60.2
IOM 44	98	39	46	51.6
IOM 45	106	48	57	55.4
IOM 46	120	48	59	61.7
IOM 47	109	45	51	56.7
IOM 48	115	49	53	61.7

IOM 49	116	45	61	59.1
IOM 50	108	47	50	56.6
IOM 51	102	44	50	56.6

Karlsruhe wreck, Orkney

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
ORK 1	82	34	46	42.6
ORK 2	82	31	42	43.7
ORK 3	86	30	43	45.7
ORK 4	76	31	39	39.3
ORK 5	82	32	40	43.5
ORK 6	70	26	38	38.1
ORK 7	88	31	44	46.4
ORK 8	82	37	40	44.6
ORK 9	89	32	41	47.6
ORK 10	84	29	41	43.7
ORK 11	116	51	61	60.2
ORK 12	102	43	52	54.1
ORK 13	110	50	53	56.7
ORK 14	98	37	49	52.0
ORK 15	102	46	51	52.3
ORK 16	84	39	48	44.8
ORK 17	123	54	60	65.6
ORK 18	112	49	51	59.8
ORK 19	103	52	52	57.0
ORK 20	114	49	57	60.4
ORK 21	49	38	49	50.8
ORK 22	97	46	51	52.3
ORK 23	106	46	57	55.2
ORK 24	97	42	51	51.3
ORK 25	101	42	52	52.7
ORK 26	107	44	52	57.0
ORK 27	105	39	52	54.2
ORK 28	99	39	51	52.2
ORK 29	98	42	49	55.1
ORK 30	89	40	49	49.3
ORK 31	127	57	69	70.3
ORK 32	111	56	57	62.8
ORK 33	109	53	58	60.9
ORK 34	115	56	54	61.5
ORK 35	129	62	66	69.2
ORK 36	115	52	58	62.4
ORK 37	117	46	52	58.2
ORK 38	112	47	53	58.7
ORK 39	123	56	56	65.5
ORK 40	121	54	58	64.1
ORK 41	105	47	59	55.0
ORK 42	93	39	52	50.7
ORK 43	106	-	51	57.5
ORK 44	95	44	51	52.1
ORK 45	99	46	48	52.7
ORK 46	92	44	49	47.6
ORK 47	105	50	54	58.0
ORK 48	85	35	44	45.4
ORK 49	99	37	50	53.0

ORK 50	94	45	50	52.3
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Skarnsundet West Bridge, Norway

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
NOR 1	106	39	56	56.0
NOR 2	111	-	51	58.0
NOR 3	118	47	49	62.1
NOR 4	115	46	54	62.2
NOR 5	115	52	58	60.7
NOR 6	109	39	51	56.8
NOR 7	108	53	52	58.6
NOR 8	111	-	51	58.2
NOR 9	123	44	52	64.4
NOR 10	111	43	55	58.1
NOR 11	105	44	50	54.6
NOR 12	126	49	54	65.1
NOR 13	108	44	51	58.7
NOR 14	106	43	49	56.8
NOR 15	102	39	49	54.1
NOR 16	129	60	59	68.9
NOR 17	123	48	59	64.9
NOR 18	103	41	46	54.7
NOR 19	99	37	54	52.1
NOR 20	97	37	44	50.5
NOR 21	121	48	53	63.8
NOR 22	120	39	56	62.8
NOR 23	102	42	50	53.2
NOR 24	101	39	47	53.0
NOR 25	31	11	15	14.8
NOR 26	96	43	45	51.4
NOR 27	111	44	54	59.3
NOR 28	113	49	54	60.9
NOR 29	95	37	48	49.4
NOR 30	96	35	51	49.0
NOR 31	90	35	43	47.6
NOR 32	87	40	41	46.6
NOR 33	77	30	40	41.5
NOR 34	125	52	59	66.8
NOR 35	133	57	62	72.1
NOR 36	99	38	52	51.9
NOR 37	96	35	45	49.9
NOR 38	106	41	48	55.2
NOR 39	110	42	53	58.3
NOR 40	111	39	48	58.6
NOR 41	119	51	53	62.1
NOR 42	95	37	46	49.8
NOR 43	115	48	49	61.4
NOR 44	100	40	44	54.0
NOR 45	114	48	52	62.0
NOR 46	120	50	59	63.8
NOR 47	94	41	46	49.9
NOR 48	109	45	47	58.6
NOR 49	103	39	50	54.2
NOR 50	111	41	47	59.1

North Llŷn Wales

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
NW 1	94	39	48	48.7
NW 2	106	45	48	57.3
NW 3	97	39	46	51.6
NW 4	87	33	41	45.3
NW 5	84	33	36	43.3
NW 6	90	38	44	47.4
NW 7	82	36	38	45.3
NW 8	82	35	40	43.8
NW 9	70	33	38	38.9
NW 10	88	41	43	47.3
NW 11	93	34	43	47.4
NW 12	81	36	37	43.3
NW 13	80	36	40	43.3
NW 14	91	40	48	48.3
NW 15	89	38	44	47.3
NW 16	97	37	40	51.5
NW 17	81	32	36	43.9
NW 18	84	31	40	43.9
NW 19	93	36	42	48.5
NW 20	81	31	39	43.2
NW 21	73	33	38	40.6
NW 22	85	35	40	44.5
NW 23	89	38	45	47.0
NW 24	81	29	38	42.3
NW 25	86	32	41	44.7
NW 26	84	36	38	45.3
NW 27	73	30	37	38.1
NW 28	73	31	38	39.4
NW 29	78	33	35	42.1
NW 30	76	28	38	39.8
NW 31	92	37	39	49.3
NW 32	99	41	48	51.2
NW 33	85	36	41	45.4
NW 34	83	32	39	44.5
NW 35	98	39	45	51.3
NW 36	101	39	47	53.1
NW 37	69	30	36	37.3
NW 38	65	27	32	33.7
NW 39	89	38	43	46.5
NW 40	93	36	45	49.4
NW 41	105	44	52	55.9
NW 42	82	38	42	44.9
NW 43	77	33	37	40.9
NW 44	88	34	40	46.7
NW 45	82	33	41	43.2
NW 46	79	33	37	42.1
NW 47	91	38	44	50.3
NW 48	83	32	37	43.7
NW 49	84	34	41	46.7
NW 50	89	33	38	47.2

Port Appin

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
PA 1	120	59	51	64.6
PA 2	94	45	52	50.9
PA 3	103	50	49	56.9
PA 4	102	45	52	54.7
PA 5	93	41	48	50.2
PA 6	103	42	48	55.0
PA 7	105	51	50	57.2
PA 8	118	49	57	62.5
PA 9	113	53	56	61.5
PA 10	110	47	54	59.2
PA 11	120	52	61	65.5
PA 12	123	56	58	67.2
PA 13	113	49	57	61.8
PA 14	117	52	52	64.6
PA 15	114	52	54	61.5
PA 16	136	57	65	74.1
PA 17	122	50	57	66.5
PA 18	123	54	64	65.5
PA 19	114	54	57	62.6
PA 20	105	45	53	55.7
PA 21	113	50	59	61.4
PA 22	102	43	52	55.0
PA 23	101	42	53	55.1
PA 24	104	50	50	58.6
PA 25	106	46	52	57.4
PA 26	87	35	41	49.3
PA 27	96	46	50	52.4
PA 28	121	52	56	65.3
PA 29	126	53	61	67.9
PA 30	102	42	53	55.1
PA 31	97	44	49	53.7
PA 32	100	48	53	53.1
PA 33	107	44	51	56.5
PA 34	115	50	57	61.6
PA 35	94	41	44	50.9
PA 36	131	56	61	70.8
PA 37	114	54	60	61.0
PA 38	99	46	48	52.8
PA 39	118	47	54	63.5
PA 40	97	45	46	52.6
PA 41	82	39	41	46.0
PA 42	98	42	47	52.5
PA 43	110	49	53	60.4
PA 44	89	39	45	48.1
PA 45	110	48	50	56.7
PA 46	95	44	45	53.0
PA 47	107	45	51	58.5
PA 48	101	49	54	56.0
PA 49	102	39	49	52.8
PA 50	105	48	57	57.6

Loch Creran

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
LC 1	106	47	52	58.3
LC 2	119	54	60	64.3
LC 3	107	55	53	59.2
LC 4	114	52	60	61.4
LC 5	112	49	57	60.7
LC 6	114	58	56	63.3
LC 7	105	51	54	58.4
LC 8	115	50	56	61.3
LC 9	134	60	63	71.6
LC 10	94	40	50	50.6
LC 11	102	46	53	55.2
LC 12	122	54	57	65.4
LC 13	109	51	53	60.6
LC 14	106	52	52	59.2
LC 15	118	53	59	63.9
LC 16	118	49	58	63.3
LC 17	128	61	67	70.2
LC 18	107	47	52	57.1
LC 19	122	51	62	65.6
LC 20	106	52	52	58.1
LC 21	113	55	59	62.8
LC 22	112	58	56	62.7
LC 23	119	50	53	64.6
LC 24	97	44	51	53.0
LC 25	113	50	52	61.7
LC 26	129	61	62	69.7
LC 27	114	51	59	63.6
LC 28	97	38	43	51.6
LC 29	110	58	54	61.5
LC 30	97	46	53	52.8
LC 31	85	38	45	47.4
LC 32	99	42	51	52.4
LC 33	105	47	54	58.2
LC 34	112	48	52	60.6
LC 35	96	42	48	52.8
LC 36	109	51	51	59.9
LC 37	87	40	44	47.4
LC 38	104	42	53	55.3
LC 39	135	53	66	71.5
LC 40	123	62	62	69.9
LC 41	107	52	54	58.4
LC 42	125	62	61	70.1
LC 43	130	57	58	72.2
LC 44	119	55	56	65.7
LC 45	115	47	54	62.1
LC 46	90	40	48	49.3
LC 47	120	54	60	65.6
LC 48	103	51	55	55.9
LC 49	110	51	59	58.8
LC 50	107	49	52	57.0

Noss Head

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
NH 1	70	25	34	35.5
NH 2	62	25	34	32.3
NH 3	58	26	33	31.4
NH 4	61	25	31	32.5
NH 5	64	26	33	33.4
NH 6	63	24	31	34.8
NH 7	68	25	33	35.5
NH 8	60	25	32	32.3
NH 9	67	27	35	35.5
NH 10	65	26	32	34.3
NH 11	59	22	31	31.3
NH 12	68	25	37	36.2
NH 13	62	22	31	31.8
NH 14	64	27	35	34.1
NH 15	63	24	31	32.3
NH 16	63	24	32	33.3
NH 17	69	27	35	37.1
NH 18	65	29	33	35.0
NH 19	68	27	33	36.2
NH 20	66	27	31	36.2
NH 21	67	25	35	35.6
NH 22	64	28	32	34.1
NH 23	59	23	30	31.7
NH 24	63	25	33	33.7
NH 25	59	24	33	32.4
NH 26	77	33	39	42.2
NH 27	77	34	40	41.3
NH 28	91	36	45	49.9
NH 29	91	33	44	49.1
NH 30	86	39	43	45.9
NH 31	117	47	54	61.6
NH 32	87	35	46	46.7
NH 33	86	34	43	45.4
NH 34	80	35	40	44.5
NH 35	82	29	40	43.3
NH 36	99	43	46	52.5
NH 37	89	34	46	48.8
NH 38	92	34	47	48.6
NH 39	100	46	49	56.5
NH 40	86	35	44	45.7
NH 41	84	32	42	45.3
NH 42	91	37	45	49.4
NH 43	88	39	43	47.8
NH 44	108	44	52	59.1
NH 45	82	36	41	44.8
NH 46	83	34	40	44.3
NH 47	90	40	45	48.0
NH 48	95	36	47	51.5
NH 49	85	31	40	44.4
NH 50	89	34	43	46.4

Dornoch Firth

Shell	Length L mm	Width W mm	Height H mm	Region length RL mm
DOR 1	126	57	66	70.0
DOR 2	117	53	56	64.5
DOR 3	115	51	55	63.4
DOR 4	117	54	58	65.5
DOR 5	65	29	34	36.4
DOR 6	125	51	61	70.0
DOR 7	118	51	62	64.5
DOR 8	123	52	61	67.6
DOR 9	116	47	63	63.5
DOR 10	113	52	58	63.5
DOR 11	113	47	64	61.4
DOR 12	107	44	53	58.3
DOR 13	87	41	44	49.9
DOR 14	96	44	47	58.2
DOR 15	120	52	61	67.6
DOR 16	114	52	56	63.5
DOR 17	118	56	57	66.6
DOR 18	118	56	59	66.6
DOR 19	105	48	56	58.2
DOR 20	127	53	63	68.7
DOR 21	117	52	62	62.4
DOR 22	87	37	44	50.0
DOR 23	113	55	57	62.4
DOR 24	106	49	57	60.0
DOR 25	111	51	52	61.4
DOR 26	97	41	56	51.0
DOR 27	116	53	59	61.4
DOR 28	106	45	57	57.2
DOR 29	100	44	54	54.1
DOR 30	105	46	55	58.3
DOR 31	118	53	61	65.5
DOR 32	75	33	43	42.7
DOR 33	104	40	56	57.2
DOR 34	117	52	55	65.5
DOR 35	110	47	58	60.0
DOR 36	125	52	63	67.6
DOR 37	122	49	55	66.6
DOR 38	120	52	62	64.5
DOR 39	109	50	58	58.2
DOR 40	97	39	52	53.1
DOR 41	118	51	59	64.5
DOR 42	119	48	58	65.6
DOR 43	120	56	64	66.6
DOR 44	116	50	61	64.5
DOR 45	70	34	39	40.0
DOR 46	107	51	54	59.3
DOR 47	109	54	52	61.4
DOR 48	76	32	45	41.6
DOR 49	100	45	52	55.2
DOR 50	104	50	52	58.3

Appendix B. North-East Atlantic horse mussel shell size data treatment

Ramsey Bay, Isle of Man horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 4$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<50	7	48.5
2	50-54.9	15	52.4
3	55-59.9	20	57.4
4	>60	9	61.5

Karlsruhe wreck, Orkney horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 8$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<40	2	38.7
2	40-44.9	6	43.8
3	45-49.9	6	47.0
4	50-54.9	14	52.3
5	55-59.9	11	57.1
6	60-64.9	7	61.7
7	65-69.9	3	66.8
8	>70	1	70.3

Skarnsundet West Bridge, Norway horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 8$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<40	1	14.8
2	40-44.9	1	41.5
3	45-49.9	7	48.9
4	50-54.9	11	53.1
5	55-59.9	14	57.9
6	60-64.9	12	62.6
7	65-69.9	3	66.9
8	>70	1	72.1

North Llŷn Wales horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 4$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<40	6	37.9
2	40-44.9	18	43.3
3	45-49.9	18	47.2
4	>50	8	52.8

Port Appin horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 6$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<50	3	46.8
2	50-54.9	12	52.5
3	55-59.9	15	56.7
4	60-64.9	12	62.2
5	65-69.9	6	66.3
6	>70	2	72.5

Loch Creran horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 6$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<50	3	48.1
2	50-54.9	6	52.2
3	55-59.9	14	57.8
4	60-64.9	16	62.4
5	65-69.9	6	67.0
6	>70	5	71.1

Noss Head horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 8$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<30	0	0
2	30-34.9	16	32.9
3	35-39.9	9	35.9
4	40-44.9	7	43.5
5	45-49.9	13	47.5
6	50-54.9	2	52.0
7	55-59.9	2	57.8
8	>60	1	61.6

Dornoch Firth horse mussel size classes based on the lengths of 50 horse mussels ($n \geq 8$)

Size classes	Shell length (mm)	No. of replicates (n)	Mean shell length
1	<40	1	36.4
2	40-44.9	3	41.4
3	45-49.9	1	49.9
4	50-54.9	4	52.1
5	55-59.9	10	57.8
6	60-64.9	17	62.7
7	65-69.9	12	66.6
8	≥ 70	2	70.0

Appendix C1.Output: SIMPER outcomes showing similarity/dissimilarity of epifaunal community within Group C in SIMPROF test. (Group A: LC, group B: DOR; group C: IOM, ORK, NOR, NW, PA, and NH)

Group C

Average similarity: 38.74

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	8.57	14.92	1.42	38.51	38.51
<i>Spirorbis tridentatus</i>	2.92	5.20	0.91	13.41	51.92
<i>Balanus balanus</i>	2.51	3.67	0.60	9.46	61.38
<i>Patinella verrucaria</i>	1.14	3.40	2.57	8.78	70.17
<i>Escharella immersa</i>	1.22	2.73	1.89	7.04	77.21
<i>Microporella ciliata</i>	1.47	1.55	1.35	4.00	81.20
<i>Tubulipora phalangea</i>	0.68	1.54	2.68	3.98	85.19
<i>Diplosolen obelia</i>	0.75	0.93	0.95	2.39	87.58
<i>Tubulipora liliacea</i>	0.42	0.87	1.15	2.23	89.81
<i>Serpula sp.</i>	0.52	0.54	0.54	1.39	91.20
<i>Plagioecia patina</i>	0.17	0.50	0.99	1.29	92.49
<i>Schizomavella linearis</i>	0.32	0.39	0.50	1.00	93.49
<i>Fenestulina malusii</i>	0.33	0.38	0.88	0.97	94.46
<i>Disporella hispida</i>	0.20	0.25	0.61	0.65	95.11
<i>Chorizopora brongniartii</i>	0.26	0.25	0.48	0.64	95.75
<i>Amphiblestrum flemingii</i>	0.22	0.19	0.48	0.50	96.25
<i>Electra pilosa</i>	0.63	0.18	0.32	0.47	96.72
<i>Scrupocellaria scruposa</i>	0.81	0.17	0.81	0.45	97.17
<i>Tubulipora plumosa</i>	0.13	0.15	0.72	0.38	97.55
<i>Callopora lineata</i>	0.15	0.14	0.68	0.36	97.91
<i>Verruca stroemia</i>	0.16	0.12	0.48	0.31	98.22
<i>Escharella variolosa</i>	0.16	0.12	0.56	0.30	98.52
<i>Crisia eburnea</i>	0.25	0.08	0.37	0.22	98.74
<i>Celleporella hyalina</i>	0.42	0.08	0.33	0.21	98.95
<i>Spirobranchus lamarckii</i>	0.07	0.07	0.60	0.17	99.12
<i>Crisia aculeata</i>	0.09	0.06	0.30	0.14	99.27
<i>Hippothoa flagellum</i>	0.05	0.06	0.51	0.14	99.41
<i>Aeta sica</i>	0.23	0.04	0.48	0.11	99.52
<i>Reptadeonella violacea</i>	0.14	0.04	0.35	0.09	99.61
<i>Stomachetosella sinuosa</i>	0.05	0.03	0.26	0.07	99.68
<i>Parasmittina trispinosa</i>	0.03	0.03	0.26	0.07	99.75
<i>Escharella klugei</i>	0.08	0.02	0.47	0.06	99.81
<i>Plagioecia sarniensis</i>	0.04	0.02	0.34	0.06	99.86
<i>Porella concinna</i>	0.07	0.02	0.34	0.04	99.90
<i>Escharella ventricosa</i>	0.01	0.01	0.45	0.04	99.94
<i>Balanus crenatus</i>	0.05	0.01	0.26	0.02	99.97
<i>Callopora craticula</i>	0.01	0.01	0.43	0.02	99.99
<i>Callopora dumerilii</i>	0.02	0.00	0.26	0.01	100.00
<i>Aetea truncata</i>	0.01	0.00	0.26	0.00	100.00

Appendix C2. Output: SIMPER outcomes showing similarity/dissimilarity of epifaunal community between Groups in SIMPROF test. (Group A: LC, group B: DOR; group C: IOM, ORK, NOR, NW, PA, and NH)

Group C & A

Average dissimilarity = 75.80

Species	Group C Av.Abund	Group A Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	8.57	4.42	24.13	24.13
<i>Balanus balanus</i>	2.51	0.03	12.58	36.71
<i>Spirorbis tridentatus</i>	2.92	0.00	11.45	48.16
<i>Escharella immersa</i>	1.22	0.02	5.41	53.58
<i>Microporella ciliata</i>	1.47	0.00	5.21	58.79
<i>Patinella verrucaria</i>	1.14	0.04	5.19	63.98
<i>Diplosolen obelia</i>	0.75	0.00	3.30	67.28
<i>Tubulipora phalangea</i>	0.68	0.01	3.14	70.42
<i>Scrupocellaria scruposa</i>	0.81	0.00	2.55	72.97
<i>Tubulipora liliacea</i>	0.42	0.00	2.22	75.19
<i>Electra pilosa</i>	0.63	0.00	2.11	77.31
<i>Serpula</i> sp.	0.52	0.00	2.02	79.33
<i>Escharoides coccinea</i>	0.39	0.00	1.78	81.10
<i>Schizomavella linearis</i>	0.32	0.00	1.63	82.74
<i>Membraniporella nitida</i>	0.35	0.00	1.60	84.34
<i>Fenestulina malusii</i>	0.33	0.00	1.34	85.67
<i>Celleporella hyalina</i>	0.42	0.00	1.25	86.93
<i>Chorizopora brongniartii</i>	0.26	0.00	1.18	88.10
<i>Plagioecia patina</i>	0.17	0.00	1.02	89.12
<i>Escharella variolosa</i>	0.16	0.00	0.98	90.11
<i>Amphiblestrum flemingii</i>	0.22	0.00	0.94	91.04
<i>Reptadeonella violacea</i>	0.14	0.00	0.88	91.92
<i>Disporella hispida</i>	0.20	0.07	0.76	92.68
<i>Crisia eburnea</i>	0.25	0.00	0.73	93.41
<i>Verruca stroemia</i>	0.16	0.00	0.72	94.13
<i>Aeta sica</i>	0.23	0.00	0.67	94.80
<i>Callopora lineata</i>	0.15	0.10	0.58	95.38
<i>Tubulipora lobifera</i>	0.12	0.00	0.57	95.95
<i>Tubulipora plumosa</i>	0.13	0.00	0.55	96.49
<i>Smittoidea reticulata</i>	0.11	0.00	0.49	96.99
<i>Crisia aculeata</i>	0.09	0.00	0.38	97.36

<i>Spirobranchus lamarckii</i>	0.07	0.00	0.27	97.64
<i>Escharella klugei</i>	0.08	0.00	0.26	97.90
<i>Stomachetosella sinuosa</i>	0.05	0.00	0.25	98.15
<i>Porella concinna</i>	0.07	0.00	0.24	98.40
<i>Hippothoa flagellum</i>	0.05	0.00	0.23	98.63
<i>Parasmittina trispinosa</i>	0.03	0.00	0.20	98.82
<i>Cellepora pumicosa</i>	0.04	0.00	0.17	98.99
<i>Balanus crenatus</i>	0.05	0.00	0.17	99.16
<i>Plagioecia sarniensis</i>	0.04	0.00	0.16	99.33
<i>Schizomavella auriculata</i>	0.02	0.00	0.12	99.45
<i>Scruparia ambiagua</i>	0.04	0.00	0.11	99.56
<i>Scruparia chelata</i>	0.03	0.00	0.09	99.65
<i>Callopora dumerilii</i>	0.02	0.00	0.07	99.71
<i>Cribrilina annulata</i>	0.02	0.00	0.06	99.78
<i>Escharella ventricosa</i>	0.01	0.00	0.06	99.84
<i>Callopora craticula</i>	0.01	0.00	0.05	99.89
<i>Aetea truncata</i>	0.01	0.00	0.04	99.93
<i>Bugula flabellata</i>	0.01	0.00	0.04	99.97
<i>Bugula turbinata</i>	0.00	0.00	0.02	99.99
<i>Aetea anguina</i>	0.00	0.00	0.00	100.00

Group C & B

Average dissimilarity = 78.45

Species	Group C Av.Abund	Group B Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	8.57	1.06	19.68	19.68
<i>Balanus crenatus</i>	0.05	3.74	12.58	32.26
<i>Balanus balanus</i>	2.51	5.14	10.98	43.24
<i>Spirorbis tridentatus</i>	2.92	0.00	8.38	51.62
<i>Conopeum reticulum</i>	0.00	1.86	6.32	57.94
<i>Celleporella hyalina</i>	0.42	1.21	3.82	61.76
<i>Patinella verrucaria</i>	1.14	0.00	3.65	65.40
<i>Microporella ciliata</i>	1.47	0.05	3.64	69.04
<i>Escharella immersa</i>	1.22	0.18	3.25	72.29
<i>Diplosolen obelia</i>	0.75	0.00	2.36	74.65
<i>Tubulipora phalangea</i>	0.68	0.00	2.20	76.85
<i>Electra pilosa</i>	0.63	0.47	2.16	79.01
<i>Scrupocellaria scruposa</i>	0.81	0.00	1.96	80.97

<i>Callopora lineata</i>	0.15	0.59	1.64	82.62
<i>Serpula</i> sp.	0.52	0.00	1.49	84.11
<i>Tubulipora liliacea</i>	0.42	0.00	1.49	85.60
<i>Escharoides coccinea</i>	0.39	0.00	1.27	86.87
<i>Membraniporella nitida</i>	0.35	0.00	1.14	88.01
<i>Schizomavella linearis</i>	0.32	0.00	1.12	89.13
<i>Fenestrulina malusii</i>	0.33	0.00	0.93	90.07
<i>Cribrilina punctata</i>	0.00	0.27	0.92	90.98
<i>Chorizopora brongniartii</i>	0.26	0.00	0.82	91.81
<i>Amphiblestrum flemingii</i>	0.22	0.00	0.68	92.49
<i>Plagioecia patina</i>	0.17	0.00	0.66	93.14
<i>Escharella variolosa</i>	0.16	0.00	0.64	93.78
<i>Disporella hispida</i>	0.20	0.00	0.59	94.38
<i>Reptadeonella violacea</i>	0.14	0.00	0.58	94.95
<i>Crisia eburnea</i>	0.25	0.00	0.57	95.53
<i>Verruca stroemia</i>	0.16	0.11	0.53	96.06
<i>Aeta sica</i>	0.23	0.00	0.53	96.59
<i>Tubulipora lobifera</i>	0.12	0.00	0.41	96.99
<i>Tubulipora plumosa</i>	0.13	0.00	0.38	97.37
<i>Smittoidea reticulata</i>	0.11	0.00	0.35	97.72
<i>Crisia aculeata</i>	0.09	0.00	0.27	97.99
<i>Callopora craticula</i>	0.01	0.09	0.27	98.26
<i>Escharella klugei</i>	0.08	0.00	0.20	98.46
<i>Spirobranchus lamarckii</i>	0.07	0.00	0.20	98.67
<i>Porella concinna</i>	0.07	0.00	0.18	98.85
<i>Stomachetosella sinuosa</i>	0.05	0.00	0.17	99.02
<i>Hippothoa flagellum</i>	0.05	0.00	0.16	99.18
<i>Cellepora pumicosa</i>	0.04	0.00	0.12	99.30
<i>Plagioecia sarniensis</i>	0.04	0.00	0.12	99.42
<i>Parasmittina trispinosa</i>	0.03	0.00	0.12	99.54
<i>Scruparia ambiugua</i>	0.04	0.00	0.09	99.63
<i>Schizomavella auriculata</i>	0.02	0.00	0.08	99.71
<i>Scruparia chelata</i>	0.03	0.00	0.07	99.78
<i>Cribrilina annulata</i>	0.02	0.00	0.05	99.83
<i>Callopora dumerilii</i>	0.02	0.00	0.05	99.88
<i>Escharella ventricosa</i>	0.01	0.00	0.04	99.92
<i>Aetea truncata</i>	0.01	0.00	0.03	99.95
<i>Bugula flabellata</i>	0.01	0.00	0.03	99.98
<i>Bugula turbinata</i>	0.00	0.00	0.01	99.99

<i>Aetea anguina</i>	0.00	0.00	0.00	100.00
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Group A & B

Average dissimilarity = 87.56

Species	Group A Av.Abund	Group B Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	0.03	5.14	29.99	29.99
<i>Balanus crenatus</i>	0.00	3.74	21.95	51`.94
<i>Spirobranchus triqueter</i>	4.42	1.06	19.72	71.65
<i>Conopeum reticulum</i>	0.00	1.86	10.92	82.57
<i>Celleporella hyalina</i>	0.00	1.21	7.10	89.67
<i>Callopora lineata</i>	0.10	0.59	2.88	92.55
<i>Electra pilosa</i>	0.00	0.47	2.76	95.31
<i>Cribrilina punctata</i>	0.00	0.27	1.58	96.89
<i>Escharella immersa</i>	0.02	0.18	0.94	97.83
<i>Verruca stroemia</i>	0.00	0.11	0.65	98.47
<i>Callopora craticula</i>	0.00	0.09	0.53	99.00
<i>Disporella hispida</i>	0.07	0.00	0.41	99.41
<i>Microporella ciliata</i>	0.00	0.05	0.29	99.71
<i>Patinella verrucaria</i>	0.04	0.00	0.23	99.94
<i>Tubulipora phalangea</i>	0.01	0.00	0.06	100.00

Appendix D1. Output: Ramsey Bay, Isle of Man SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1

Average similarity: 47.77

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	3.35	17.79	1.99	37.25	37.25
<i>Microporella ciliata</i>	1.90	9.76	1.76	20.42	57.67
<i>Electra pilosa</i>	1.07	3.97	0.80	8.31	65.99
<i>Celleporella hyalina</i>	0.91	2.73	0.73	5.71	71.70
<i>Aeta sica</i>	0.82	2.57	0.64	5.38	77.08
<i>Escharella immersa</i>	0.68	2.33	0.51	4.87	81.94
<i>Patinella verrucaria</i>	0.93	2.16	0.51	4.53	86.47
<i>Crisia eburnea</i>	0.77	2.07	0.55	4.34	90.81

Region 2

Average similarity: 41.14

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.79	22.38	2.14	54.39	54.39
<i>Microporella ciliata</i>	1.21	5.90	0.90	14.34	68.74
<i>Electra pilosa</i>	0.80	3.19	0.56	7.75	76.49
<i>Spirorbis tridentatus</i>	0.71	1.99	0.39	4.84	81.33
<i>Celleporella hyalina</i>	0.64	1.66	0.42	4.03	85.36
<i>Patinella verrucaria</i>	0.56	1.59	0.38	3.88	89.24
<i>Aeta sica</i>	0.46	1.07	0.33	2.60	91.84

Region 3

Average similarity: 28.51

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	1.65	8.77	0.81	30.77	30.77
<i>Microporella ciliata</i>	1.20	7.14	0.80	25.05	55.82
<i>Electra pilosa</i>	0.83	6.03	0.58	21.13	76.95
<i>Escharella immersa</i>	0.43	1.86	0.32	6.53	83.48
<i>Fenestrulina malusii</i>	0.52	1.34	0.36	4.71	88.19
<i>Celleporella hyalina</i>	0.50	1.27	0.35	4.47	92.65

Region 4

Average similarity: 41.59

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.69	21.24	1.64	51.06	51.06
<i>Microporella ciliata</i>	1.12	6.82	0.90	16.40	67.46
<i>Electra pilosa</i>	0.98	6.28	0.66	15.11	82.57
<i>Spirorbis tridentatus</i>	0.82	2.42	0.38	5.82	88.40
<i>Celleporella hyalina</i>	0.54	1.56	0.40	3.75	92.14

Appendix D2. Output: Ramsey Bay, Isle of Man SIMPER outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 57.71

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	3.35	2.79	12.97	12.97
<i>Microporella ciliata</i>	1.90	1.21	9.67	22.64
<i>Electra pilosa</i>	1.07	0.80	7.74	30.38
<i>Patinella verrucaria</i>	0.93	0.56	7.52	37.90
<i>Spirorbis tridentatus</i>	0.64	0.71	7.08	44.97
<i>Celleporella hyalina</i>	0.91	0.64	6.97	51.95
<i>Aeta sica</i>	0.82	0.46	6.44	58.39
<i>Crisia eburnea</i>	0.77	0.50	6.15	64.54
<i>Escharella immersa</i>	0.68	0.08	5.65	70.19
<i>Balanus balanus</i>	0.45	0.43	5.00	75.19
<i>Fenestrulina malusii</i>	0.64	0.27	4.94	80.13
<i>Tubulipora phalangea</i>	0.33	0.22	3.15	83.28
<i>Chorizopora brongniartii</i>	0.14	0.21	2.46	85.74
<i>Tubulipora plumosa</i>	0.20	0.12	2.14	87.88
<i>Callopora lineata</i>	0.24	0.11	2.10	89.98
<i>Crisia aculeata</i>	0.13	0.18	1.96	91.94

Regions 1 & 3

Average dissimilarity = 66.90.

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	3.35	1.65	19.09	19.09
<i>Microporella ciliata</i>	1.90	1.20	10.24	29.33
<i>Electra pilosa</i>	1.07	0.83	7.58	36.91
<i>Patinella verrucaria</i>	0.93	0.40	7.20	44.11
<i>Celleporella hyalina</i>	0.91	0.50	6.50	50.61
<i>Escharella immersa</i>	0.68	0.43	6.32	56.93
<i>Aeta sica</i>	0.82	0.12	6.23	63.16
<i>Fenestrulina malusii</i>	0.64	0.52	5.50	68.66
<i>Crisia eburnea</i>	0.77	0.03	5.48	74.14
<i>Spirorbis tridentatus</i>	0.64	0.25	4.96	79.10

<i>Balanus balanus</i>	0.45	0.02	3.49	82.59
<i>Tubulipora phalangea</i>	0.33	0.25	3.25	85.84
<i>Tubulipora plumosa</i>	0.20	0.23	2.55	88.39
<i>Callopora lineata</i>	0.24	0.11	2.12	90.51

Regions 2 & 3

Average dissimilarity = 69.23

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.79	1.65	20.31	20.31
<i>Microporella ciliata</i>	1.21	1.20	10.68	30.99
<i>Electra pilosa</i>	0.80	0.83	8.88	39.88
<i>Spirorbis tridentatus</i>	0.71	0.25	7.29	47.16
<i>Celleporella hyalina</i>	0.64	0.50	6.79	53.95
<i>Patinella verrucaria</i>	0.56	0.40	6.56	60.51
<i>Fenestrulina malusii</i>	0.27	0.52	5.01	65.52
<i>Escharella immersa</i>	0.08	0.43	4.72	70.24
<i>Aeta sica</i>	0.46	0.12	4.44	74.68
<i>Balanus balanus</i>	0.43	0.02	3.90	78.57
<i>Crisia eburnea</i>	0.50	0.03	3.84	82.41
<i>Chorizopora brongniartii</i>	0.21	0.16	3.00	85.41
<i>Tubulipora phalangea</i>	0.22	0.25	2.99	88.40
<i>Tubulipora plumosa</i>	0.12	0.23	2.34	90.74

Regions 1 & 4

Average dissimilarity = 59.08

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	3.35	2.69	15.03	15.03
<i>Microporella ciliata</i>	1.90	1.12	9.75	24.79
<i>Electra pilosa</i>	1.07	0.98	8.18	32.97
<i>Spirorbis tridentatus</i>	0.64	0.82	8.02	40.98
<i>Patinella verrucaria</i>	0.93	0.37	7.36	48.34
<i>Celleporella hyalina</i>	0.91	0.54	6.76	55.10
<i>Aeta sica</i>	0.82	0.23	6.41	61.52
<i>Escharella immersa</i>	0.68	0.32	6.28	67.80
<i>Crisia eburnea</i>	0.77	0.02	5.69	73.49

<i>Fenestrulina malusii</i>	0.64	0.39	5.38	78.87
<i>Balanus balanus</i>	0.45	0.09	3.79	82.66
<i>Tubulipora phalangea</i>	0.33	0.13	2.91	85.57
<i>Tubulipora plumosa</i>	0.20	0.10	2.10	87.67
<i>Callopora lineata</i>	0.24	0.09	2.07	89.74
<i>Chorizopora brongniartii</i>	0.14	0.17	2.07	91.81

Regions 2 & 4

Average dissimilarity = 59.46

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.79	2.69	16.14	16.14
<i>Spirorbis tridentatus</i>	0.71	0.82	10.51	26.65
<i>Microporella ciliata</i>	1.21	1.12	10.34	36.99
<i>Electra pilosa</i>	0.80	0.98	10.01	47.00
<i>Celleporella hyalina</i>	0.64	0.54	7.32	54.33
<i>Patinella verrucaria</i>	0.56	0.37	6.50	60.82
<i>Aeta sica</i>	0.46	0.23	5.04	65.86
<i>Fenestrulina malusii</i>	0.27	0.39	4.66	70.52
<i>Balanus balanus</i>	0.43	0.09	4.27	74.79
<i>Crisia eburnea</i>	0.50	0.02	4.07	78.86
<i>Escharella immersa</i>	0.08	0.32	3.78	82.65
<i>Chorizopora brongniartii</i>	0.21	0.17	3.14	85.78
<i>Tubulipora phalangea</i>	0.22	0.13	2.49	88.28
<i>Crisia aculeata</i>	0.18	0.08	1.91	90.19

Regions 3 & 4

Average dissimilarity = 66.83

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	1.65	2.69	22.69	22.69
<i>Microporella ciliata</i>	1.20	1.12	11.77	34.46
<i>Electra pilosa</i>	0.83	0.98	11.31	45.77
<i>Spirorbis tridentatus</i>	0.25	0.82	9.04	54.81
<i>Celleporella hyalina</i>	0.50	0.54	6.74	61.55
<i>Escharella immersa</i>	0.43	0.32	6.72	68.27
<i>Fenestrulina malusii</i>	0.52	0.39	6.19	74.46

<i>Patinella verrucaria</i>	0.40	0.37	5.86	80.32
<i>Aeta sica</i>	0.12	0.23	2.85	83.17
<i>Tubulipora phalangea</i>	0.25	0.13	2.76	85.93
<i>Chorizopora brongniartii</i>	0.16	0.17	2.65	88.58
<i>Tubulipora plumosa</i>	0.23	0.10	2.42	91.00

Appendix D3. Output: Karlsruhe wreck, Orkney outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1
Average similarity: 20.90

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.89	6.19	0.52	29.64	29.64
<i>Balanus balanus</i>	0.86	6.12	0.44	29.28	58.92
<i>Patinella verrucaria</i>	0.67	4.50	0.46	21.51	80.43
<i>Tubulipora liliacea</i>	0.33	1.20	0.24	5.73	86.16
<i>Escharella immersa</i>	0.27	0.62	0.17	2.97	89.13
<i>Tubulipora phalangea</i>	0.30	0.56	0.18	2.68	91.81
<i>Microporella ciliata</i>	0.29	0.54	0.18	2.60	94.41
<i>Fenestrulina malusii</i>	0.17	0.45	0.14	2.14	96.54
<i>Plagioecia patina</i>	0.20	0.28	0.13	1.34	97.88
<i>Diplosolen obelia</i>	0.13	0.23	0.11	1.09	98.97
<i>Tubulipora plumosa</i>	0.11	0.15	0.09	0.71	99.69
<i>Spirorbis tridentatus</i>	0.10	0.05	0.07	0.23	99.92
<i>Electra pilosa</i>	0.04	0.01	0.03	0.04	99.96
<i>Parasmittina trispinosa</i>	0.04	0.01	0.03	0.04	100.00

Region 2
Average similarity: 20.07

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.93	11.46	0.63	57.10	57.10
<i>Balanus balanus</i>	0.69	4.35	0.43	21.67	78.77
<i>Patinella verrucaria</i>	0.38	2.67	0.29	13.30	92.06
<i>Escharella immersa</i>	0.21	0.44	0.15	2.17	94.24

<i>Fenestrulina malusii</i>	0.15	0.36	0.13	1.78	96.02
<i>Microporella ciliata</i>	0.17	0.29	0.11	1.43	97.45
<i>Parasmittina trispinosa</i>	0.11	0.16	0.09	0.77	98.22
<i>Spirorbis tridentatus</i>	0.13	0.13	0.09	0.65	98.87
<i>Tubulipora liliacea</i>	0.09	0.13	0.07	0.64	99.52
<i>Tubulipora phalangea</i>	0.07	0.05	0.05	0.25	99.77
<i>Plagioecia patina</i>	0.05	0.02	0.03	0.11	99.88
<i>Callopora lineata</i>	0.04	0.02	0.03	0.08	99.96
<i>Escharella variolosa</i>	0.05	0.01	0.03	0.04	100.00

Region 3

Average similarity: 2.21

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.14	0.52	0.11	23.66	23.66
<i>Microporella ciliata</i>	0.14	0.40	0.12	18.08	41.74
<i>Spirorbis tridentatus</i>	0.18	0.38	0.16	17.15	58.88
<i>Patinella verrucaria</i>	0.17	0.34	0.12	15.15	74.03
<i>Fenestrulina malusii</i>	0.08	0.24	0.08	10.78	84.81
<i>Escharella immersa</i>	0.10	0.10	0.10	4.73	89.54
<i>Plagioecia patina</i>	0.08	0.08	0.07	3.77	93.31
<i>Tubulipora phalangea</i>	0.08	0.07	0.07	3.35	96.66
<i>Tubulipora liliacea</i>	0.06	0.07	0.07	3.34	100.00

Region 4

Average similarity: 10.17

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.39	6.38	0.37	62.73	62.73
<i>Patinella verrucaria</i>	0.25	1.54	0.21	15.16	77.89
<i>Balanus balanus</i>	0.20	1.30	0.16	12.82	90.71
<i>Microporella ciliata</i>	0.20	0.35	0.12	3.46	94.17
<i>Spirorbis tridentatus</i>	0.17	0.28	0.11	2.80	96.97
<i>Tubulipora phalangea</i>	0.11	0.09	0.08	0.86	97.83
<i>Tubulipora liliacea</i>	0.09	0.08	0.05	0.77	98.60
<i>Escharella immersa</i>	0.07	0.06	0.05	0.62	99.23

<i>Plagioecia patina</i>	0.06	0.03	0.05	0.34	99.56
<i>Fenestrulina malusii</i>	0.05	0.03	0.03	0.26	99.82
<i>Tubulipora plumosa</i>	0.06	0.02	0.03	0.18	100.00

Appendix D4. Output: Karlsruhe wreck, Orkney outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 80.09

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.89	0.93	20.69	20.69
<i>Balanus balanus</i>	0.86	0.69	19.78	40.47
<i>Patinella verrucaria</i>	0.67	0.38	14.03	54.50
<i>Tubulipora liliacea</i>	0.33	0.09	6.53	61.02
<i>Escharella immersa</i>	0.27	0.21	6.24	67.27
<i>Microporella ciliata</i>	0.29	0.17	5.80	73.07
<i>Fenestrulina malusii</i>	0.17	0.15	4.85	77.92
<i>Tubulipora phalangea</i>	0.30	0.07	4.63	82.55
<i>Plagioecia patina</i>	0.20	0.05	3.27	85.82
<i>Diplosolen obelia</i>	0.13	0.3	2.61	88.44
<i>Spirorbis tridentatus</i>	0.10	0.13	2.48	90.91
<i>Parasmittina trispinosa</i>	0.04	0.11	1.92	92.83
<i>Tubulipora plumosa</i>	0.11	0.00	1.85	94.69
<i>Callopora lineata</i>	0.02	0.04	1.73	96.42
<i>Escharella variolosa</i>	0.03	0.05	0.86	97.28
<i>Scrupocellaria scruposa</i>	0.02	0.06	0.72	98.00
<i>Electra pilosa</i>	0.04	0.00	0.64	98.64
<i>Schizomavella linearis</i>	0.02	0.03	0.52	99.16
<i>Reptadeonella violacea</i>	0.00	0.03	0.33	99.50
<i>Hippothoa flagellum</i>	0.00	0.02	0.33	99.82
<i>Escharella ventricosa</i>	0.02	0.00	0.18	100.00

Regions 1 & 3

Average dissimilarity = 95.62

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	0.86	0.03	20.77	20.77
<i>Spirobranchus triqueter</i>	0.89	0.14	19.04	39.81
<i>Patinella verrucaria</i>	0.67	0.17	14.85	54.66
<i>Tubulipora liliacea</i>	0.33	0.06	7.41	62.07
<i>Microporella ciliata</i>	0.29	0.14	6.20	68.27
<i>Escharella immersa</i>	0.27	0.10	5.88	74.16
<i>Tubulipora phalangea</i>	0.30	0.08	4.84	79.00
<i>Fenestulina malusii</i>	0.17	0.08	4.83	83.83
<i>Plagioecia patina</i>	0.20	0.08	3.47	87.31
<i>Diplosolen obelia</i>	0.13	0.02	2.91	90.21
<i>Spirorbis tridentatus</i>	0.10	0.018	2.56	92.77
<i>Tubulipora plumosa</i>	0.11	0.02	2.30	95.08
<i>Callopora lineata</i>	0.02	0.00	1.79	96.87
<i>Escharella variolosa</i>	0.03	0.04	0.78	97.65
<i>Electra pilosa</i>	0.04	0.00	0.78	98.43
<i>Parasmittina trispinosa</i>	0.04	0.00	0.44	98.87
<i>Schizomavella linearis</i>	0.02	0.02	0.39	99.26
<i>Chorizopora brongniartii</i>	0.00	0.03	0.25	99.50
<i>Scrupocellaria scruposa</i>	0.02	0.00	0.18	99.68
<i>Escharella ventricosa</i>	0.02	0.00	0.18	99.86
<i>Reptadeonella violacea</i>	0.00	0.02	0.14	100.00

Regions 2 & 3

Average dissimilarity = 95.43

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.93	0.14	30.86	30.86
<i>Balanus balanus</i>	0.69	0.03	16.35	47.21
<i>Patinella verrucaria</i>	0.38	0.17	14.66	61.87
<i>Microporella ciliata</i>	0.17	0.14	5.91	67.78
<i>Fenestulina malusii</i>	0.15	0.08	5.35	73.13
<i>Escharella immersa</i>	0.21	0.10	4.63	77.75
<i>Spirorbis tridentatus</i>	0.13	0.18	4.23	81.99
<i>Tubulipora liliacea</i>	0.09	0.06	4.17	86.16

<i>Tubulipora phalangea</i>	0.07	0.08	2.55	88.71
<i>Plagioecia patina</i>	0.05	0.08	2.45	91.16
<i>Parasmittina trispinosa</i>	0.11	0.00	2.32	93.49
<i>Diplosolen obelia</i>	0.03	0.02	1.45	94.94
<i>Callopora lineata</i>	0.04	0.00	1.34	96.28
<i>Escharella variolosa</i>	0.05	0.04	0.88	97.16
<i>Scrupocellaria scruposa</i>	0.06	0.00	0.70	97.86
<i>Reptadeonella violacea</i>	0.03	0.02	0.60	98.45
<i>Schizomavella linearis</i>	0.03	0.02	0.53	98.99
<i>Hippothoa flagellum</i>	0.02	0.00	0.51	99.49
<i>Chorizopora brongiartii</i>	0.00	0.03	0.30	99.80
<i>Tubulipora plumosa</i>	0.00	0.02	0.20	100.00

Regions 1 & 4

Average dissimilarity = 87.45

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	0.86	0.20	20.61	20.61
<i>Spirobranchus triqueter</i>	0.89	0.39	19.74	40.35
<i>Patinella verrucaria</i>	0.67	0.25	14.80	55.15
<i>Tubulipora liliacea</i>	0.33	0.09	7.24	62.40
<i>Microporella ciliata</i>	0.29	0.20	6.46	68.86
<i>Escharella immersa</i>	0.27	0.07	5.69	74.55
<i>Tubulipora phalangea</i>	0.30	0.11	5.05	79.60
<i>Fenestulina malusii</i>	0.17	0.05	4.21	83.81
<i>Plagioecia patina</i>	0.20	0.06	3.19	87.00
<i>Spirorbis tridentatus</i>	0.10	0.17	3.03	90.03
<i>Tubulipora plumosa</i>	0.11	0.06	3.01	93.03
<i>Diplosolen obelia</i>	0.13	0.00	2.44	95.47
<i>Callopora lineata</i>	0.02	0.00	1.46	96.93
<i>Parasmittina trispinosa</i>	0.04	0.02	0.82	97.75
<i>Electra pilosa</i>	0.04	0.00	0.73	98.49
<i>Escharella variolosa</i>	0.03	0.02	0.69	99.18
<i>Schizomavella linearis</i>	0.02	0.00	0.25	99.43
<i>Reptadeonella violacea</i>	0.00	0.02	0.21	99.64
<i>Scrupocellaria scruposa</i>	0.02	0.00	0.18	99.82
<i>Escharella ventricosa</i>	0.02	0.00	0.18	100.00

Regions 2 & 4

Average dissimilarity = 86.04

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.93	0.39	29.02	29.02
<i>Balanus balanus</i>	0.69	0.20	18.65	47.68
<i>Patinella verrucaria</i>	0.38	0.25	14.88	62.56
<i>Microporella ciliata</i>	0.17	0.20	6.20	68.76
<i>Escharella immersa</i>	0.21	0.07	4.76	73.51
<i>Spirorbis tridentatus</i>	0.13	0.17	4.65	78.16
<i>Fenestrulina malusii</i>	0.15	0.05	4.22	82.37
<i>Tubulipora liliacea</i>	0.09	0.09	4.08	86.45
<i>Tubulipora phalangea</i>	0.07	0.11	2.74	89.19
<i>Parasmittina trispinosa</i>	0.11	0.02	2.60	91.79
<i>Plagioecia patina</i>	0.05	0.06	1.91	93.70
<i>Tubulipora plumosa</i>	0.00	0.06	1.47	95.16
<i>Callopora lineata</i>	0.04	0.00	1.17	96.33
<i>Escharella variolosa</i>	0.05	0.02	0.77	97.10
<i>Diplosolen obelia</i>	0.03	0.00	0.75	97.84
<i>Scrupocellaria scruposa</i>	0.06	0.00	0.68	98.52
<i>Reptadeonella violacea</i>	0.03	0.02	0.66	99.18
<i>Hippothoa flagellum</i>	0.02	0.00	0.47	99.65
<i>Schizomavella linearis</i>	0.03	0.00	0.35	100.00

Regions 3 & 4

Average dissimilarity 95.88

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.14	0.39	28.36	28.36
<i>Patinella verrucaria</i>	0.17	0.25	15.13	43.48
<i>Balanus balanus</i>	0.03	0.20	13.47	56.96
<i>Microporella ciliata</i>	0.14	0.20	8.48	65.43
<i>Spirorbis tridentatus</i>	0.18	0.17	7.35	72.78
<i>Fenestrulina malusii</i>	0.08	0.05	5.19	77.98
<i>Tubulipora liliacea</i>	0.06	0.09	5.11	83.09
<i>Tubulipora phalangea</i>	0.08	0.11	3.55	86.64
<i>Tubulipora plumosa</i>	0.02	0.06	3.37	90.00
<i>Escharella immersa</i>	0.10	0.07	3.33	93.34

<i>Plagioecia patina</i>	0.08	0.06	2.58	95.91
<i>Diplosolen obelia</i>	0.02	0.00	1.09	97.00
<i>Parasmittina trispinosa</i>	0.00	0.02	0.90	97.90
<i>Escharella variolosa</i>	0.04	0.02	0.84	98.74
<i>Reptadeonella violacea</i>	0.02	0.02	0.60	99.35
<i>Chorizopora brongniartii</i>	0.03	0.00	0.41	99.76
<i>Schizomavella linearis</i>	0.02	0.00	0.24	100.00

Appendix D5. Output: Skarnsundet West Bridge, Norway SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1

Average similarity: 45.54

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.58	21.00	2.08	46.10	46.10
<i>Spirorbis tridentatus</i>	1.71	9.78	1.15	21.47	67.57
<i>Tubulipora phalangea</i>	1.07	4.93	0.79	10.83	78.40
<i>Tubulipora liliacea</i>	0.82	4.17	0.65	9.16	87.56
<i>Serpula sp.</i>	0.66	1.64	0.41	3.59	91.15
<i>Patinella verrucaria</i>	0.42	0.89	0.35	1.95	93.10
<i>Diplosolen obelia</i>	0.38	0.83	0.27	1.82	94.93
<i>Disporella hispida</i>	0.36	0.71	0.30	1.56	96.49
<i>Escharella immersa</i>	0.32	0.59	0.25	1.29	97.77
<i>Amphiblestrum flemingii</i>	0.25	0.34	0.21	0.74	98.52
<i>Plagioecia patina</i>	0.18	0.16	0.13	0.34	98.86
<i>Balanus balanus</i>	0.14	0.13	0.11	0.29	99.15
<i>Tubulipora plumosa</i>	0.14	0.13	0.11	0.28	99.43
<i>Schizomavella linearis</i>	0.12	0.10	0.11	0.22	99.65
<i>Microporella ciliata</i>	0.10	0.04	0.07	0.09	99.74
<i>Spirobranchus lamarckii</i>	0.11	0.04	0.07	0.09	99.82
<i>Callopora craticula</i>	0.08	0.04	0.07	0.08	99.91
<i>Callopora dumerilii</i>	0.06	0.02	0.05	0.04	99.95
<i>Parasmittina trispinosa</i>	0.07	0.02	0.05	0.03	99.98
<i>Stomachetosella sinuosa</i>	0.04	0.01	0.03	0.02	100.00

Region 2
Average similarity: 49.22

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	3.07	31.38	2.41	63.76	63.76
<i>Spirorbis tridentatus</i>	1.57	10.53	1.20	21.39	85.14
<i>Tubulipora phalangea</i>	0.66	2.10	0.49	4.27	89.41
<i>Serpula sp.</i>	0.61	1.49	0.39	3.02	92.43
<i>Patinella verrucaria</i>	0.42	1.03	0.34	2.10	94.53
<i>Tubulipora liliacea</i>	0.31	0.64	0.25	1.30	95.83
<i>Disporella hispida</i>	0.26	0.52	0.23	1.06	96.89
<i>Diplosolen obelia</i>	0.23	0.40	0.18	0.80	97.70
<i>Plagioecia patina</i>	0.23	0.29	0.17	0.60	98.30
<i>Escharella immersa</i>	0.17	0.21	0.14	0.43	98.73
<i>Balanus balanus</i>	0.17	0.19	0.13	0.39	99.12
<i>Schizomavella linearis</i>	0.16	0.15	0.13	0.30	99.42
<i>Amphiblestrum flemingii</i>	0.16	0.14	0.13	0.28	99.70
<i>Callopora dumerilii</i>	0.09	0.05	0.07	0.10	99.79
<i>Stomachetosella sinuosa</i>	0.08	0.02	0.05	0.05	99.84
<i>Microporella ciliata</i>	0.06	0.02	0.05	0.04	99.88
<i>Spirobranchus lamarckii</i>	0.07	0.02	0.05	0.04	99.93
<i>Tubulipora plumosa</i>	0.07	0.02	0.05	0.04	99.96
<i>Escharella klugei</i>	0.04	0.01	0.03	0.01	99.98
<i>Parasmittina trispinosa</i>	0.05	0.01	0.03	0.01	99.99
<i>Callopora craticula</i>	0.04	0.01	0.03	0.01	100.00

Region 3
Average similarity: 11.16

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.71	6.52	0.45	58.42	58.42
<i>Spirorbis tridentatus</i>	0.54	3.01	0.35	27.00	85.41
<i>Tubulipora phalangea</i>	0.27	0.91	0.21	8.12	93.53
<i>Tubulipora liliacea</i>	0.14	0.28	0.09	2.54	96.07
<i>Diplosolen obelia</i>	0.13	0.21	0.07	1.87	97.94

<i>Patinella verrucaria</i>	0.04	0.07	0.03	0.61	98.56
<i>Spirobranchus lamarckii</i>	0.06	0.05	0.05	0.47	99.03
<i>Escharella immersa</i>	0.07	0.05	0.05	0.43	99.46
<i>Serpula sp.</i>	0.04	0.02	0.03	0.16	99.63
<i>Amphiblestrum flemingii</i>	0.04	0.02	0.03	0.14	99.76
<i>Dispirella hispida</i>	0.05	0.01	0.03	0.12	99.89
<i>Schizomavella linearis</i>	0.04	0.01	0.03	0.11	100.00

Region 4

Average similarity: 25.46

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	1.56	16.14	0.80	63.36	63.36
<i>Spirorbis tridentatus</i>	0.94	7.23	0.59	28.39	91.75
<i>Serpula sp.</i>	0.24	0.46	0.17	1.82	93.57
<i>Tubulipora liliacea</i>	0.24	0.45	0.18	1.77	95.34
<i>Tubulipora phalangea</i>	0.18	0.33	0.15	1.29	96.63
<i>Patinella verrucaria</i>	0.14	0.32	0.13	1.28	97.91
<i>Dispirella hispida</i>	0.15	0.28	0.12	1.10	99.01
<i>Diplosolen obelia</i>	0.13	0.19	0.11	0.76	99.77
<i>Microporella ciliata</i>	0.06	0.03	0.05	0.12	99.89
<i>Spirobranchus lamarckii</i>	0.07	0.03	0.05	0.11	100.00

Appendix D6. Output: Skarnsundet West Bridge, Norway outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 53.95

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.58	3.07	15.79	15.79
<i>Spirorbis tridentatus</i>	1.71	1.57	14.38	30.17
<i>Tubulipora phalangea</i>	1.07	0.66	10.62	40.79
<i>Tubulipora liliacea</i>	0.82	0.31	9.01	49.79
<i>Serpula sp.</i>	0.66	0.61	8.70	58.49
<i>Patinella verrucaria</i>	0.42	0.42	5.80	64.29

<i>Diplosolen obelia</i>	0.38	0.23	5.27	69.57
<i>Disporella hispida</i>	0.36	0.26	4.63	74.20
<i>Escharella immersa</i>	0.32	0.17	4.04	78.24
<i>Plagioecia patina</i>	0.18	0.23	3.55	81.79
<i>Amphiblestrum flemingii</i>	0.25	0.16	3.17	84.96
<i>Balanus balanus</i>	0.14	0.17	2.97	87.93
<i>Schizomavella linearis</i>	0.12	0.16	2.39	90.32
<i>Tubulipora plumosa</i>	0.14	0.07	1.93	92.26
<i>Spirobranchus lamarckii</i>	0.11	0.07	1.53	93.79
<i>Microporella ciliata</i>	0.10	0.06	1.36	95.15
<i>Callopora dumerilii</i>	0.06	0.09	1.35	96.50
<i>Stomachetosella sinuosa</i>	0.04	0.08	1.18	97.68
<i>Callopora craticula</i>	0.08	0.04	1.00	98.68
<i>Parasmittina trispinosa</i>	0.07	0.05	0.93	99.61
<i>Escharella klugei</i>	0.00	0.04	0.39	100.00

Regions 1 & 3

Average dissimilarity = 81.50

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.58	0.71	26.82	26.82
<i>Spirorbis tridentatus</i>	1.71	0.54	16.82	43.64
<i>Tubulipora phalangea</i>	1.07	0.27	11.45	55.09
<i>Tubulipora liliacea</i>	0.82	0.14	10.14	65.23
<i>Serpula sp.</i>	0.66	0.04	6.17	71.39
<i>Diplosolen obelia</i>	0.38	0.13	4.87	76.27
<i>Patinella verrucaria</i>	0.42	0.04	3.86	80.13
<i>Escharella immersa</i>	0.32	0.07	3.41	83.54
<i>Disporella hispida</i>	0.36	0.05	3.30	86.84
<i>Amphiblestrum flemingii</i>	0.25	0.04	2.31	89.15
<i>Plagioecia patina</i>	0.18	0.02	1.92	91.08
<i>Tubulipora plumosa</i>	0.14	0.02	1.63	92.71
<i>Balanus balanus</i>	0.14	0.00	1.58	94.29
<i>Schizomavella linearis</i>	0.12	0.04	1.40	95.70
<i>Spirobranchus lamarckii</i>	0.11	0.06	1.36	97.06
<i>Microporella ciliata</i>	0.10	0.00	0.80	97.85
<i>Callopora craticula</i>	0.08	0.00	0.69	98.55
<i>Parasmittina trispinosa</i>	0.07	0.00	0.53	99.08

<i>Callopora dumerilii</i>	0.06	0.00	0.51	99.59
<i>Stomachetosella sinuosa</i>	0.04	0.00	0.41	100.00

Regions 2 & 3

Average dissimilarity = 80.98

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	3.07	0.71	36.75	36.75
<i>Spirorbis tridentatus</i>	1.57	0.54	17.22	53.97
<i>Tubulipora phalangea</i>	0.66	0.27	7.53	61.50
<i>Serpula sp.</i>	0.61	0.04	5.92	67.42
<i>Tubulipora liliacea</i>	0.31	0.14	4.56	71.98
<i>Patinella verrucaria</i>	0.42	0.04	4.55	76.53
<i>Diplosolen obelia</i>	0.23	0.13	3.93	80.47
<i>Disporella hispida</i>	0.26	0.05	3.32	83.79
<i>Plagioecia patina</i>	0.23	0.02	2.59	86.38
<i>Escharella immersa</i>	0.17	0.07	2.44	88.82
<i>Balanus balanus</i>	0.17	0.00	2.07	90.90
<i>Schizomavella linearis</i>	0.16	0.04	1.87	92.76
<i>Amphiblestrum flemingii</i>	0.16	0.04	1.79	94.52
<i>Spirobranchus lamarckii</i>	0.07	0.06	1.19	95.72
<i>Callopora dumerilii</i>	0.09	0.00	0.95	96.66
<i>Stomachetosella sinuosa</i>	0.08	0.00	0.88	97.54
<i>Tubulipora plumosa</i>	0.07	0.02	0.71	98.25
<i>Microporella ciliata</i>	0.06	0.00	0.64	98.90
<i>Escharella klugei</i>	0.04	0.00	0.43	99.33
<i>Parasmittina trispinosa</i>	0.05	0.00	0.37	99.71
<i>Callopora craticula</i>	0.04	0.00	0.29	100.00

Regions 1 & 4

Average dissimilarity = 69.29

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.58	1.56	23.11	23.11
<i>Spirorbis tridentatus</i>	1.71	0.94	16.62	39.73
<i>Tubulipora phalangea</i>	1.07	0.18	11.42	51.15
<i>Tubulipora liliacea</i>	0.82	0.24	10.21	61.36

<i>Serpula</i> sp.	0.66	0.24	7.24	68.61
<i>Diplosolen obelia</i>	0.38	0.13	4.83	73.44
<i>Patinella verrucaria</i>	0.42	0.14	4.50	77.93
<i>Disporella hispida</i>	0.36	0.15	4.10	82.03
<i>Escharella immersa</i>	0.32	0.02	3.28	85.31
<i>Amphiblestrum flemingii</i>	0.25	0.02	2.31	87.62
<i>Plagioecia patina</i>	0.18	0.03	2.15	89.78
<i>Balanus balanus</i>	0.14	0.02	1.76	91.54
<i>Tubulipora plumosa</i>	0.14	0.02	1.71	93.25
<i>Spirobranchus lamarckii</i>	0.11	0.07	1.51	94.76
<i>Schizomavella linearis</i>	0.12	0.02	1.35	96.11
<i>Microporella ciliata</i>	0.10	0.06	1.34	97.45
<i>Callopora craticula</i>	0.08	0.00	0.73	98.18
<i>Parasmittina trispinosa</i>	0.07	0.00	0.57	98.75
<i>Stomachetosella sinuosa</i>	0.04	0.02	0.56	99.32
<i>Callopora dumerilii</i>	0.06	0.00	0.54	99.86
<i>Escharella klugei</i>	0.00	0.02	0.14	100.00

Regions 2 & 4

Average dissimilarity = 66.49

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	3.07	1.56	30.98	30.98
<i>Spirorbis tridentatus</i>	1.57	0.94	17.42	48.41
<i>Tubulipora phalangea</i>	0.66	0.18	7.64	56.05
<i>Serpula</i> sp.	0.61	0.24	7.36	63.40
<i>Patinella verrucaria</i>	0.42	0.14	5.31	68.71
<i>Tubulipora liliacea</i>	0.31	0.24	5.29	74.00
<i>Disporella hispida</i>	0.26	0.15	4.22	78.21
<i>Diplosolen obelia</i>	0.23	0.13	3.88	82.09
<i>Plagioecia patina</i>	0.23	0.03	2.93	85.02
<i>Balanus balanus</i>	0.17	0.02	2.33	87.35
<i>Escharella immersa</i>	0.17	0.02	2.16	89.52
<i>Schizomavella linearis</i>	0.16	0.02	1.87	91.39
<i>Amphiblestrum flemingii</i>	0.16	0.02	1.74	93.13
<i>Spirobranchus lamarckii</i>	0.07	0.07	1.36	94.49
<i>Microporella ciliata</i>	0.06	0.06	1.25	95.74
<i>Stomachetosella sinuosa</i>	0.08	0.02	1.08	96.82

<i>Callopora dumerilii</i>	0.09	0.00	1.02	97.84
<i>Tubulipora plumosa</i>	0.07	0.02	0.82	98.65
<i>Escharella klugei</i>	0.04	0.02	0.61	99.26
<i>Parasmittina trispinosa</i>	0.05	0.00	0.41	99.67
<i>Callopora craticula</i>	0.04	0.00	0.33	100.00

Regions 3 & 4

Average dissimilarity = 83.50

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.71	1.56	37.50	37.50
<i>Spirorbis tridentatus</i>	0.54	0.94	23.03	60.53
<i>Tubulipora phalangea</i>	0.27	0.18	6.83	67.36
<i>Tubulipora liliacea</i>	0.14	0.24	6.43	73.78
<i>Diplosolen obelia</i>	0.13	0.13	5.10	78.88
<i>Patinella verrucaria</i>	0.04	0.14	4.47	83.35
<i>Serpula</i> sp.	0.04	0.24	4.35	87.70
<i>Disporella hispida</i>	0.05	0.15	4.08	91.78
<i>Spirobranchus lamarckii</i>	0.06	0.07	1.98	93.76
<i>Escharella immersa</i>	0.07	0.02	1.44	95.20
<i>Microporella ciliata</i>	0.00	0.06	1.05	96.25
<i>Amphiblestrum flemingii</i>	0.04	0.02	1.00	97.25
<i>Plagioecia patina</i>	0.02	0.03	0.83	98.08
<i>Schizomavella linearis</i>	0.04	0.02	0.76	98.83
<i>Tubulipora plumosa</i>	0.02	0.02	0.49	99.32
<i>Balanus balanus</i>	0.00	0.02	0.28	99.60
<i>Escharella klugei</i>	0.00	0.02	0.20	99.80
<i>Stomachetosella sinuosa</i>	0.00	0.02	0.20	100.00

Appendix D7. Output: North Llŷn Wales SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1

Average similarity: 28.61

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Balanus balanus</i>	1.62	9.39	0.76	32.82	32.82
<i>Escharella immersa</i>	0.69	5.24	0.64	18.31	51.13
<i>Spirobranchus triqueter</i>	0.76	3.68	0.58	12.86	63.99

<i>Escharella variolosa</i>	0.54	3.04	0.52	10.63	74.63
<i>Schizomavella linearis</i>	0.39	1.59	0.37	5.56	80.18
<i>Reptadeonella violacea</i>	0.37	1.27	0.31	4.43	84.61
<i>Chorizopora brongniartii</i>	0.33	0.97	0.30	3.41	88.02
<i>Patinella verrucaria</i>	0.30	0.97	0.27	3.39	91.40
<i>Electra pilosa</i>	0.33	0.83	0.27	2.90	94.31
<i>Tubulipora liliacea</i>	0.21	0.29	0.17	1.02	95.33
<i>Diplosolen obelia</i>	0.20	0.28	0.15	0.96	96.29
<i>Microporella ciliata</i>	0.15	0.20	0.13	0.70	96.99
<i>Serpula sp.</i>	0.15	0.17	0.13	0.59	97.59
<i>Disporella hispida</i>	0.13	0.14	0.11	0.50	98.08
<i>Verruca stroemia</i>	0.10	0.14	0.09	0.48	98.56
<i>Stomachetosella sinuosa</i>	0.12	0.09	0.09	0.32	98.89
<i>Schizomavella auriculata</i>	0.09	0.06	0.07	0.22	99.11
<i>Tubulipora phalangea</i>	0.10	0.06	0.07	0.19	99.30
<i>Plagioecia patina</i>	0.08	0.05	0.07	0.18	99.48
<i>Hippothoa flagellum</i>	0.08	0.05	0.07	0.16	99.64
<i>Scrupocellaria scruposa</i>	0.08	0.03	0.05	0.11	99.75
<i>Fenestrulina malusii</i>	0.06	0.03	0.05	0.10	99.85
<i>Crisia aculeata</i>	0.11	0.02	0.03	0.06	99.90
<i>Bugula flabellata</i>	0.04	0.01	0.03	0.04	99.94
<i>Aeta sica</i>	0.05	0.01	0.03	0.03	99.97
<i>Crisia eburnea</i>	0.05	0.01	0.03	0.03	100.00

Region 2

Average similarity: 32.68

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Balanus balanus</i>	1.94	9.16	0.82	28.02	28.02
<i>Spirobranchus triqueter</i>	1.29	8.01	0.98	24.50	52.52
<i>Escharella immersa</i>	0.72	3.29	0.64	10.06	62.58
<i>Escharella variolosa</i>	0.53	2.48	0.49	7.60	70.18
<i>Schizomavella linearis</i>	0.50	2.17	0.48	6.64	76.82

<i>Reptadeonella violacea</i>	0.47	2.03	0.43	6.21	83.03
<i>Patinella verrucaria</i>	0.51	1.70	0.40	5.19	88.22
<i>Chorizopora brongniartii</i>	0.39	0.91	0.29	2.77	90.99
<i>Electra pilosa</i>	0.37	0.70	0.27	2.14	93.14
<i>Diplosolen obelia</i>	0.27	0.53	0.23	1.63	94.77
<i>Tubulipora phalangea</i>	0.20	0.29	0.17	0.89	95.66
<i>Stomachetosella sinuosa</i>	0.18	0.29	0.17	0.87	96.53
<i>Plagioecia patina</i>	0.16	0.24	0.13	0.72	97.25
<i>Microporella ciliata</i>	0.17	0.19	0.15	0.57	97.82
<i>Tubulipora liliacea</i>	0.16	0.16	0.11	0.49	98.30
<i>Disporella hispida</i>	0.14	0.15	0.11	0.45	98.76
<i>Fenestrulina malusii</i>	0.15	0.14	0.13	0.44	99.20
<i>Verruca stroemia</i>	0.12	0.10	0.09	0.30	99.50
<i>Schizomavella auriculata</i>	0.10	0.08	0.09	0.23	99.73
<i>Scrupocellaria scruposa</i>	0.07	0.02	0.05	0.05	99.78
<i>Hippothoa flagellum</i>	0.07	0.02	0.05	0.05	99.83
<i>Escharella ventricosa</i>	0.04	0.01	0.03	0.04	99.87
<i>Aeta sica</i>	0.04	0.01	0.03	0.03	99.90
<i>Spirorbis tridentatus</i>	0.07	0.01	0.03	0.03	99.93
<i>Callopora lineata</i>	0.04	0.01	0.03	0.02	99.95
<i>Escharella klugei</i>	0.04	0.01	0.03	0.02	99.97
<i>Crisia aculeata</i>	0.07	0.01	0.03	0.02	99.99
<i>Serpula sp.</i>	0.05	0.00	0.03	0.01	100.00

Region 3

Average similarity: 4.05

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Reptadeonella violacea</i>	0.14	2.03	0.16	50.03	50.03
<i>Spirobranchus triqueter</i>	0.19	0.83	0.14	20.51	70.54
<i>Escharella immersa</i>	0.12	0.59	0.10	14.47	85.00
<i>Chorizopora brongniartii</i>	0.14	0.31	0.10	7.69	92.70
<i>Escharella variolosa</i>	0.07	0.12	0.06	2.99	95.69

<i>Electra pilosa</i>	0.08	0.07	0.06	1.70	97.38
<i>Plagioecia patina</i>	0.04	0.04	0.03	1.02	98.40
<i>Tubulipora phalangea</i>	0.04	0.04	0.03	0.91	99.31
<i>Tubulipora liliacea</i>	0.04	0.03	0.03	0.69	100.00

Region 4

Average similarity: 12.45

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Escharella immersa</i>	0.41	3.58	0.34	28.72	28.72
<i>Spirobranchus triqueter</i>	0.55	3.11	0.44	24.97	53.69
<i>Reptadeonella violacea</i>	0.36	2.49	0.30	19.99	73.68
<i>Schizomavella linearis</i>	0.22	0.61	0.20	4.94	78.61
<i>Electra pilosa</i>	0.20	0.57	0.15	4.62	83.23
<i>Balanus balanus</i>	0.27	0.53	0.18	4.24	87.47
<i>Chorizopora brongniartii</i>	0.23	0.49	0.18	3.90	91.37
<i>Microporella ciliata</i>	0.18	0.34	0.16	2.77	94.14
<i>Escharella variolosa</i>	0.12	0.22	0.09	1.75	95.89
<i>Tubulipora liliacea</i>	0.11	0.12	0.10	0.94	96.83
<i>Patinella verrucaria</i>	0.13	0.10	0.07	0.84	97.67
<i>Plagioecia patina</i>	0.09	0.08	0.07	0.67	98.34
<i>Hippothoa flagellum</i>	0.08	0.08	0.07	0.64	98.98
<i>Porella concinna</i>	0.04	0.04	0.03	0.31	99.29
<i>Tubulipora phalangea</i>	0.07	0.03	0.05	0.26	99.55
<i>Disporella hispida</i>	0.04	0.02	0.03	0.12	99.67
<i>Stomachetosella sinuosa</i>	0.04	0.01	0.03	0.11	99.79
<i>Verruca stroemia</i>	0.04	0.01	0.03	0.11	99.90
<i>Diplosolen obelia</i>	0.04	0.01	0.03	0.10	100.00

Appendix D8. Output: North Llŷn Wales outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 69.41

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	1.62	1.94	17.10	17.10
<i>Spirobranchus triqueter</i>	0.76	1.29	10.10	27.20
<i>Escharella immersa</i>	0.69	0.72	6.87	34.07
<i>Escharella variolosa</i>	0.54	0.53	6.09	40.15
<i>Patinella verrucaria</i>	0.30	0.51	5.46	45.61
<i>Reptadeonella violacea</i>	0.37	0.47	5.45	51.06
<i>Schizomavella linearis</i>	0.39	0.50	5.26	56.32
<i>Chorizopora brongniartii</i>	0.33	0.39	4.81	61.13
<i>Electra pilosa</i>	0.33	0.37	4.55	65.68
<i>Diplosolen obelia</i>	0.20	0.27	3.48	69.17
<i>Tubulipora liliacea</i>	0.21	0.16	2.94	72.11
<i>Tubulipora phalangea</i>	0.10	0.20	2.30	74.41
<i>Stomachetosella sinuosa</i>	0.12	0.18	2.27	76.68
<i>Disporella hispida</i>	0.13	0.14	2.27	78.96
<i>Microporella ciliata</i>	0.15	0.17	2.25	81.21
<i>Plagioecia patina</i>	0.08	0.16	2.17	83.38
<i>Verruca stroemia</i>	0.10	0.12	2.02	85.41
<i>Fenestrulina malusii</i>	0.06	0.15	1.59	87.00
<i>Schizomavella auriculata</i>	0.09	0.10	1.52	88.52
<i>Serpula sp.</i>	0.15	0.05	1.43	89.96
<i>Crisia aculeate</i>	0.11	0.07	1.23	91.19
<i>Hippothoa flagellum</i>	0.08	0.07	1.08	92.27
<i>Scrupocellaria scruposa</i>	0.08	0.07	1.07	93.34
<i>Aeta sica</i>	0.05	0.04	0.82	94.16
<i>Spirorbis tridentatus</i>	0.02	0.07	0.71	94.87
<i>Crisia eburnea</i>	0.05	0.03	0.62	95.48
<i>Bugula flabellata</i>	0.04	0.03	0.61	96.09
<i>Bugula turbinata</i>	0.02	0.02	0.59	96.69
<i>Escharella ventricosa</i>	0.02	0.04	0.58	97.27
<i>Callopora lineata</i>	0.02	0.04	0.51	97.78
<i>Balanus crenatus</i>	0.03	0.02	0.45	98.23

<i>Porella concinna</i>	0.02	0.02	0.45	98.68
<i>Spirobranchus lamarckii</i>	0.02	0.02	0.32	99.00
<i>Tubulipora plumosa</i>	0.02	0.02	0.29	99.29
<i>Escharella klugei</i>	0.00	0.04	0.28	99.58
<i>Celleporella hyalina</i>	0.03	0.00	0.24	99.82
<i>Plagioecia sarniensis</i>	0.02	0.00	0.18	100.00

Regions 1 & 3

Average dissimilarity = 94.03

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	1.62	0.02	19.99	19.99
<i>Escharella immersa</i>	0.69	0.12	11.60	31.58
<i>Spirobranchus triqueter</i>	0.76	0.19	9.41	41.00
<i>Escharella variolosa</i>	0.54	0.07	7.74	48.73
<i>Reptadeonella violacea</i>	0.37	0.14	6.18	54.91
<i>Schizomavella linearis</i>	0.39	0.00	5.02	59.94
<i>Chorizopora brongniartii</i>	0.33	0.14	4.67	64.60
<i>Patinella verrucaria</i>	0.30	0.02	4.42	69.02
<i>Electra pilosa</i>	0.33	0.08	4.19	73.21
<i>Diplosolen obelia</i>	0.20	0.00	2.45	75.66
<i>Tubulipora liliacea</i>	0.21	0.04	2.41	78.07
<i>Microporella ciliata</i>	0.15	0.03	1.89	79.96
<i>Disporella hispida</i>	0.13	0.03	1.72	81.68
<i>Verruca stroemia</i>	0.10	0.00	1.68	83.36
<i>Bugula turbinata</i>	0.02	0.00	1.56	84.92
<i>Serpula sp.</i>	0.15	0.00	1.51	86.43
<i>Stomachetosella sinuosa</i>	0.12	0.02	1.49	87.92
<i>Tubulipora phalangea</i>	0.10	0.04	1.46	89.38
<i>Schizomavella auriculata</i>	0.09	0.02	1.40	90.78
<i>Plagioecia patina</i>	0.08	0.04	1.35	92.13
<i>Crisia aculeata</i>	0.11	0.00	1.05	93.18
<i>Scrupocellaria scruposa</i>	0.08	0.00	0.87	94.05
<i>Hippothoa flagellum</i>	0.08	0.00	0.81	94.86
<i>Fenestrulina malusii</i>	0.06	0.00	0.74	95.60
<i>Porella concinna</i>	0.02	0.02	0.72	96.32
<i>Aeta sica</i>	0.05	0.00	0.58	96.90
<i>Crisia eburnea</i>	0.05	0.00	0.57	97.47

<i>Bugula flabellata</i>	0.04	0.00	0.49	97.95
<i>Balanus crenatus</i>	0.03	0.00	0.46	98.42
<i>Celleporella hyalina</i>	0.03	0.00	0.31	98.73
<i>Callopora lineata</i>	0.02	0.00	0.26	98.98
<i>Plagioecia sarniensis</i>	0.02	0.00	0.24	99.23
<i>Spirorbis tridentatus</i>	0.02	0.00	0.21	99.43
<i>Tubulipora plumosa</i>	0.02	0.00	0.21	99.64
<i>Spirobranchus lamarckii</i>	0.02	0.00	0.18	99.82
<i>Escharella ventricosa</i>	0.02	0.00	0.18	100.00

Regions 2 &3

Average dissimilarity = 93.64

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	1.94	0.02	19.21	19.21
<i>Spirobranchus triqueter</i>	1.29	0.19	14.05	33.26
<i>Escharella immersa</i>	0.72	0.12	7.47	40.73
<i>Escharella variolosa</i>	0.53	0.07	6.63	47.36
<i>Reptadeonella violacea</i>	0.47	0.14	6.46	53.83
<i>Patinella verrucaria</i>	0.51	0.02	5.69	59.52
<i>Schizomavella linearis</i>	0.50	0.00	5.54	65.06
<i>Chorizopora brongniartii</i>	0.39	0.14	4.87	69.93
<i>Electra pilosa</i>	0.37	0.08	3.95	73.88
<i>Tubulipora liliacea</i>	0.16	0.04	3.19	77.07
<i>Diplosolen obelia</i>	0.27	0.00	2.75	79.82
<i>Plagioecia patina</i>	0.16	0.04	2.53	82.34
<i>Tubulipora phalangea</i>	0.20	0.04	2.45	84.80
<i>Stomachetosella sinuosa</i>	0.18	0.02	1.98	86.77
<i>Disporella hispida</i>	0.14	0.02	1.75	88.52
<i>Microporella ciliata</i>	0.17	0.03	1.55	90.07
<i>Verruca stroemia</i>	0.12	0.00	1.41	91.48
<i>Fenestulina malusii</i>	0.15	0.00	1.33	92.81
<i>Schizomavella auriculata</i>	0.10	0.02	1.15	93.97
<i>Porella concinna</i>	0.02	0.02	0.61	94.57
<i>Spirorbis tridentatus</i>	0.07	0.00	0.60	95.17
<i>Escharella ventricosa</i>	0.04	0.00	0.60	95.77
<i>Hippothoa flagellum</i>	0.07	0.00	0.53	96.30
<i>Scrupocellaria scruposa</i>	0.07	0.00	0.50	96.80

<i>Aeta sica</i>	0.04	0.00	0.49	97.29
<i>Crisia aculeata</i>	0.07	0.00	0.43	97.72
<i>Callopora lineata</i>	0.04	0.00	0.38	98.10
<i>Bugula flabellata</i>	0.03	0.00	0.32	98.42
<i>Serpula sp.</i>	0.05	0.00	0.31	98.73
<i>Escharella klugei</i>	0.04	0.00	0.30	99.03
<i>Bugula turbinata</i>	0.02	0.00	0.26	99.29
<i>Spirobranchus lamarckii</i>	0.02	0.00	0.21	99.50
<i>Crisia eburnea</i>	0.03	0.00	0.18	99.68
<i>Balanus crenatus</i>	0.02	0.00	0.18	99.86
<i>Tubulipora plumosa</i>	0.02	0.00	0.14	100.00

Regions 1 &4

Average dissimilarity = 84.11

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	1.62	0.27	18.31	18.31
<i>Escharella immersa</i>	0.69	0.41	10.02	28.33
<i>Spirobranchus triqueter</i>	0.76	0.55	9.31	37.64
<i>Escharella variolosa</i>	0.54	0.12	7.15	44.79
<i>Reptadeonella violacea</i>	0.37	0.36	6.72	51.52
<i>Schizomavella linearis</i>	0.39	0.22	5.38	56.89
<i>Electra pilosa</i>	0.33	0.20	4.75	61.65
<i>Chorizopora brongniartii</i>	0.33	0.23	4.67	66.32
<i>Patinella verrucaria</i>	0.30	0.13	4.65	70.97
<i>Microporella ciliata</i>	0.15	0.18	2.80	73.77
<i>Tubulipora liliacea</i>	0.21	0.11	2.66	76.42
<i>Diplosolen obelia</i>	0.20	0.04	2.53	78.95
<i>Disporella hispida</i>	0.13	0.04	1.86	80.81
<i>Verruca stroemia</i>	0.10	0.04	1.79	82.60
<i>Plagioecia patina</i>	0.08	0.09	1.57	84.17
<i>Stomachetosella sinuosa</i>	0.12	0.04	1.54	85.71
<i>Tubulipora phalangea</i>	0.10	0.07	1.50	87.21
<i>Serpula sp</i>	0.15	0.00	1.43	88.64
<i>Hippothoa flagellum</i>	0.08	0.08	1.42	90.06
<i>Schizomavella auriculata</i>	0.09	0.02	1.25	91.31
<i>Bugula turbinata</i>	0.02	0.00	1.15	92.46
<i>Crisia aculeata</i>	0.11	0.00	1.00	93.46

<i>Porella concinna</i>	0.02	0.04	0.90	94.36
<i>Fenestrulina malusii</i>	0.06	0.02	0.82	95.18
<i>Scrupocellaria scruposa</i>	0.08	0.00	0.81	95.99
<i>Balanus crenatus</i>	0.03	0.02	0.55	96.54
<i>Aeta sica</i>	0.05	0.00	0.55	97.09
<i>Crisia eburnea</i>	0.05	0.00	0.54	97.63
<i>Bugula flabellata</i>	0.04	0.00	0.45	98.08
<i>Spirorbis tridentatus</i>	0.02	0.02	0.35	98.43
<i>Celleporella hyalina</i>	0.03	0.00	0.29	98.72
<i>Escharella klugei</i>	0.00	0.02	0.27	98.99
<i>Callopora lineata</i>	0.02	0.00	0.24	99.23
<i>Plagioecia sarniensis</i>	0.02	0.00	0.23	99.46
<i>Tubulipora plumosa</i>	0.02	0.00	0.20	99.65
<i>Spirobranchus lamarckii</i>	0.02	0.00	0.17	99.83
<i>Escharella ventricosa</i>	0.02	0.00	0.17	100.00

Regions 2 &4

Average dissimilarity = 83.36

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	1.94	0.27	17.99	17.99
<i>Spirobranchus triqueter</i>	1.29	0.55	12.33	30.32
<i>Escharella immersa</i>	0.72	0.41	7.59	37.91
<i>Reptadeonella violacea</i>	0.47	0.36	6.65	44.57
<i>Escharella variolosa</i>	0.53	0.12	6.28	50.85
<i>Patinella verrucaria</i>	0.51	0.13	5.78	56.63
<i>Schizomavella linearis</i>	0.50	0.22	5.58	62.21
<i>Chorizopora brongniartii</i>	0.39	0.23	4.89	67.10
<i>Electra pilosa</i>	0.37	0.20	4.49	71.59
<i>Tubulipora liliacea</i>	0.16	0.11	3.09	74.68
<i>Diplosolen obelia</i>	0.27	0.04	2.79	77.48
<i>Plagioecia patina</i>	0.16	0.09	2.58	80.06
<i>Microporella ciliata</i>	0.17	0.18	2.45	82.51
<i>Tubulipora phalangea</i>	0.20	0.07	2.42	84.93
<i>Stomachetosella sinuosa</i>	0.18	0.04	1.98	86.91
<i>Disporella hispida</i>	0.14	0.04	1.87	88.78
<i>Verruca stroemia</i>	0.12	0.04	1.60	90.38
<i>Fenestrulina malusii</i>	0.15	0.02	1.40	91.78

<i>Hippothoa flagellum</i>	0.07	0.08	1.15	92.92
<i>Schizomavella auriculata</i>	0.10	0.02	1.07	94.00
<i>Porella concinna</i>	0.02	0.04	0.78	94.78
<i>Spirorbis tridentatus</i>	0.07	0.02	0.72	95.50
<i>Escharella ventricosa</i>	0.04	0.00	0.55	96.05
<i>Escharella klugei</i>	0.04	0.02	0.52	96.57
<i>Scrupocellaria scruposa</i>	0.07	0.00	0.49	97.06
<i>Aeta sica</i>	0.04	0.00	0.46	97.52
<i>Crisia aculeata</i>	0.07	0.00	0.43	97.95
<i>Callopora lineata</i>	0.04	0.00	0.36	98.32
<i>Serpula sp.</i>	0.05	0.00	0.32	98.63
<i>Bugula flabellata</i>	0.03	0.00	0.31	98.94
<i>Balanus crenatus</i>	0.02	0.02	0.30	99.24
<i>Bugula turbinata</i>	0.02	0.00	0.24	99.48
<i>Spirobranchus lamarckii</i>	0.02	0.00	0.20	99.68
<i>Crisia eburnea</i>	0.03	0.00	0.18	99.86
<i>Tubulipora plumosa</i>	0.02	0.00	0.14	100.00

Regions 3 &4

Average dissimilarity = 93.36

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Escharella immersa</i>	0.12	0.41	17.16	17.16
<i>Reptadeonella violacea</i>	0.14	0.36	16.60	33.76
<i>Spirobranchus triqueter</i>	0.19	0.55	13.89	47.65
<i>Chorizopora brongniartii</i>	0.14	0.23	6.76	54.40
<i>Electra pilosa</i>	0.08	0.20	6.43	60.83
<i>Escharella variolosa</i>	0.07	0.12	5.42	66.25
<i>Balanus balanus</i>	0.02	0.27	5.15	71.40
<i>Schizomavella linearis</i>	0.00	0.22	3.99	75.39
<i>Microporella ciliata</i>	0.03	0.18	3.22	78.61
<i>Porella concinna</i>	0.02	0.04	3.05	81.66
<i>Plagioecia patina</i>	0.04	0.09	2.70	84.36
<i>Patinella verrucaria</i>	0.02	0.13	2.66	87.02
<i>Tubulipora liliacea</i>	0.04	0.11	2.44	89.46
<i>Tubulipora phalangea</i>	0.04	0.07	2.17	91.63
<i>Hippothoa flagellum</i>	0.00	0.08	1.59	93.22
<i>Disporella hispida</i>	0.02	0.04	1.52	94.74

<i>Schizomavella auriculata</i>	0.02	0.02	1.21	95.95
<i>Stomachetosella sinuosa</i>	0.02	0.04	1.15	97.10
<i>Escharella klugei</i>	0.00	0.02	0.73	97.83
<i>Verruca stroemia</i>	0.00	0.04	0.72	98.55
<i>Diplosolen obelia</i>	0.00	0.04	0.67	99.22
<i>Spirorbis tridentatus</i>	0.00	0.02	0.27	99.49
<i>Fenestrulina malusii</i>	0.00	0.02	0.27	99.76
<i>Balanus crenatus</i>	0.00	0.02	0.24	100.00

Appendix D9. Output: Port Appin SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1

Average similarity: 46.16

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.75	15.54	2.07	33.67	33.67
<i>Scrupocellaria scruposa</i>	1.61	7.66	1.02	16.59	50.26
<i>Balanus balanus</i>	1.72	7.08	1.07	15.35	65.60
<i>Spirorbis tridentatus</i>	1.21	3.52	0.69	7.62	73.22
<i>Serpula sp.</i>	0.67	2.12	0.57	4.60	77.82
<i>Escharella immersa</i>	0.67	1.97	0.57	4.27	82.09
<i>Diplosolen obelia</i>	0.64	1.90	0.54	4.12	86.21
<i>Patinella verrucaria</i>	0.62	1.85	0.53	4.00	90.21
<i>Microporella ciliata</i>	0.73	1.82	0.55	3.95	94.16
<i>Amphiblestrum flemingii</i>	0.32	0.54	0.30	1.18	95.34
<i>Tubulipora phalangea</i>	0.30	0.41	0.26	0.88	96.22
<i>Dispirella hispida</i>	0.32	0.35	0.23	0.76	96.99
<i>Crisia eburnea</i>	0.25	0.00	0.21	0.71	97.70
<i>Callopora lineata</i>	0.28	0.33	0.21	0.71	98.41
<i>Verruca stroemia</i>	0.20	0.25	0.18	0.54	98.95
<i>Escharella klugei</i>	0.18	0.12	0.13	0.27	99.21
<i>Spirobranchus lamarckii</i>	0.12	0.09	0.11	0.21	99.42
<i>Porella concinna</i>	0.14	0.09	0.13	0.20	99.62
<i>Cribrilina annulata</i>	0.12	0.05	0.09	0.11	99.74

<i>Tubulipora liliacea</i>	0.8	0.03	0.07	0.07	99.81
<i>Hippothoa flagellum</i>	0.9	0.03	0.07	0.07	99.88
<i>Balanus crenatus</i>	0.8	0.03	0.07	0.06	99.94
<i>Chorizopora brongniartii</i>	0.7	0.01	0.05	0.02	99.96
<i>Plagioecia patina</i>	0.4	0.01	0.03	0.01	99.98
<i>Fenestrulina malusii</i>	0.4	0.01	0.03	0.01	99.99
<i>Plagioecia sarniensis</i>	0.5	0.01	0.03	0.01	100.00

Region 2

Average similarity: 52.07

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.92	17.67	2.98	33.93	33.93
<i>Balanus balanus</i>	2.05	11.15	1.41	21.42	55.35
<i>Scrupocellaria scruposa</i>	1.72	8.33	1.18	16.00	71.35
<i>Spirorbis tridentatus</i>	1.32	5.05	0.94	9.69	81.05
<i>Escharella immersa</i>	0.72	2.64	0.67	5.08	86.12
<i>Serpula</i> sp.	0.57	1.66	0.48	3.20	89.32
<i>Microporella ciliata</i>	0.62	1.55	0.49	2.98	92.30
<i>Porella concinna</i>	0.40	1.04	0.39	2.00	94.30
<i>Patinella verrucaria</i>	0.44	1.00	0.36	1.91	96.21
<i>Diplosolen obelia</i>	0.43	0.89	0.37	1.71	97.93
<i>Disporella hispida</i>	0.22	0.25	0.19	0.47	98.40
<i>Escharella klugei</i>	0.19	0.23	0.17	0.44	98.84
<i>Crisia eburnea</i>	0.19	0.16	0.15	0.30	99.14
<i>Verruca stroemia</i>	0.14	0.15	0.13	0.29	99.43
<i>Spirobranchus lamarckii</i>	0.11	0.05	0.09	0.10	99.53
<i>Chorizopora brongniartii</i>	0.11	0.05	0.09	0.09	99.62
<i>Aeta sica</i>	0.09	0.03	0.07	0.07	99.69
<i>Plagioecia sarniensis</i>	0.08	0.03	0.07	0.06	99.75
<i>Callopora lineata</i>	0.10	0.03	0.07	0.06	99.81
<i>Amphiblestrum flemingii</i>	0.09	0.03	0.07	0.05	99.86
<i>Balanus crenatus</i>	0.11	0.02	0.05	0.05	88.91

<i>Tubulipora liliacea</i>	0.06	0.01	0.05	0.03	99.93
<i>Tubulipora phalangea</i>	0.07	0.01	0.05	0.03	99.96
<i>Escharella ventricosa</i>	0.04	0.01	0.03	0.01	99.97
<i>Hippothoa flagellum</i>	0.04	0.00	0.03	0.01	99.98
<i>Cribrilina annulata</i>	0.04	0.00	0.03	0.01	99.99
<i>Fenestrulina malusii</i>	0.04	0.00	0.03	0.01	100.00

Region 3
Average similarity: 11.12

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.87	5.60	0.48	50.31	50.31
<i>Spirorbis tridentatus</i>	0.60	1.77	0.33	15.93	66.24
<i>Microporella ciliata</i>	0.36	1.51	0.27	13.62	79.86
<i>Escharella immersa</i>	0.25	0.45	0.16	4.05	83.91
<i>Patinella verrucaria</i>	0.20	0.33	0.15	2.95	86.86
<i>Escharella klugei</i>	0.18	0.31	0.09	2.79	89.65
<i>Serpula</i> sp.	0.17	0.24	0.13	2.17	91.83
<i>Balanus balanus</i>	0.15	0.18	0.11	1.66	93.49
<i>Scrupocellaria scruposa</i>	0.14	0.16	0.11	1.45	94.94
<i>Disporella hispida</i>	0.10	0.12	0.09	1.09	96.02
<i>Tubulipora phalangea</i>	0.12	0.11	0.09	1.00	97.03
<i>Callopora lineata</i>	0.11	0.09	0.09	0.78	97.81
<i>Porella concinna</i>	0.08	0.06	0.07	0.53	98.35
<i>Diplosolen obelia</i>	0.10	0.06	0.07	0.51	98.86
<i>Chorizopora brongniartii</i>	0.10	0.04	0.08	0.40	99.26
<i>Tubulipora liliacea</i>	0.07	0.04	0.05	0.34	99.60
<i>Amphiblestrum flemingii</i>	0.06	0.04	0.05	0.33	99.93
<i>Cribrilina annulata</i>	0.04	0.01	0.03	0.07	100.00

Region 4
Average similarity: 28.71

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.07	13.03	1.01	45.37	45.37

<i>Spirorbis tridentatus</i>	1.11	5.62	0.70	19.56	64.93
<i>Serpula sp.</i>	0.46	1.76	0.27	6.12	71.05
<i>Escharella immersa</i>	0.59	1.70	0.38	5.93	76.98
<i>Microporella ciliata</i>	0.59	1.63	0.40	5.67	82.64
<i>Balanus balanus</i>	0.52	1.43	0.32	4.99	87.63
<i>Scrupocellaria scruposa</i>	0.55	1.32	0.33	4.60	92..23
<i>Diplosolen obelia</i>	0.34	1.01	0.27	3.51	95.74
<i>Patinella verrucaria</i>	0.32	0.49	0.25	1.71	97.46
<i>Tubulipora phalangea</i>	0.20	0.22	0.17	0.77	98.23
<i>Callopora lineata</i>	0.18	0.17	0.13	0.59	98.82
<i>Porella concinna</i>	0.12	0.12	0.10	0.41	99.23
<i>Chorizopora brongniartii</i>	0.11	0.06	0.09	0.20	99.42
<i>Crisia eburnea</i>	0.11	0.04	0.07	0.14	99.57
<i>Escharella klugei</i>	0.09	0.03	0.07	0.11	99.68
<i>Disporella hispida</i>	0.06	0.03	0.05	0.11	99.79
<i>Balanus crenatus</i>	0.09	0.02	0.05	0.07	99.96
<i>Fenestrulina malusii</i>	0.04	0.01	0.03	0.03	99.88
<i>Cribrilina annulata</i>	0.04	0.01	0.03	0.02	99.91
<i>Tubulipora plumosa</i>	0.05	0.01	0.03	0.02	99.93
<i>Hippothoa flagellum</i>	0.05	0.01	0.03	0.02	99.95
<i>Aeta sica</i>	0.04	0.00	0.03	0.02	99.97
<i>Amphiblestrum flemingii</i>	0.04	0.00	0.03	0.02	99.98
<i>Tubulipora liliacea</i>	0.04	0.00	0.03	0.02	100.00

Appendix D10. Output: Port Appin outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 51.37

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	1.72	2.05	12.12	12.12

<i>Spirobranchus triqueter</i>	2.75	2.92	10.06	22.18
<i>Scrupocellaria scruposa</i>	1.61	1.72	9.81	31.98
<i>Spirorbis tridentatus</i>	1.21	1.32	9.36	41.34
<i>Microporella ciliata</i>	0.73	0.62	6.05	47.40
<i>Escharella immersa</i>	0.67	0.72	5.63	53.02
<i>Serpula</i> sp.	0.67	0.57	5.51	58.53
<i>Patinella verrucaria</i>	0.62	0.44	5.15	63.68
<i>Diplosolen obelia</i>	0.64	0.43	5.13	68.81
<i>Porella concinna</i>	0.14	0.40	3.23	72.04
<i>Disporella hispida</i>	0.32	0.22	3.06	75.10
<i>Crisia eburnea</i>	0.25	0.19	2.71	77.81
<i>Amphiblestrum flemingii</i>	0.32	0.09	2.53	80.34
<i>Callopora lineata</i>	0.28	0.10	2.43	82.78
<i>Escharella klugei</i>	0.18	0.19	2.36	85.14
<i>Tubulipora phalangea</i>	0.30	0.07	2.30	87.44
<i>Verruca stroemia</i>	0.20	0.14	2.19	89.63
<i>Spirobranchus lamarckii</i>	0.12	0.11	1.51	91.14
<i>Balanus crenatus</i>	0.08	0.11	1.37	92.51
<i>Chorizopora brongniartii</i>	0.07	0.11	1.07	93.59
<i>Cribrilina annulata</i>	0.12	0.04	1.01	94.60
<i>Tubulipora liliacea</i>	0.08	0.06	0.92	95.52
<i>Hippothoa flagellum</i>	0.09	0.04	0.87	96.39
<i>Plagioecia sarniensis</i>	0.05	0.08	0.86	97.25
<i>Aeta sica</i>	0.03	0.09	0.81	98.06
<i>Fenestulina malusii</i>	0.04	0.04	0.55	98.60
<i>Escharella ventricosa</i>	0.02	0.04	0.44	99.05
<i>Plagioecia patina</i>	0.04	0.00	0.31	99.36
<i>Crisia aculeata</i>	0.02	0.02	0.26	99.62
<i>Celleporella hyalina</i>	0.00	0.02	0.14	99.76
<i>Aetea truncata</i>	0.02	0.00	0.14	99.90
<i>Callopora craticula</i>	0.02	0.00	0.10	100.00

Regions 1 & 3

Average dissimilarity = 82.93

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.75	0.87	17.46	17.46
<i>Balanus balanus</i>	1.72	0.15	13.30	30.76

<i>Scrupocellaria scruposa</i>	1.61	1.14	12.65	43.41
<i>Spirorbis tridentatus</i>	1.21	0.60	8.42	51.83
<i>Serpula sp.</i>	0.67	0.17	5.32	57.15
<i>Microporella ciliata</i>	0.73	0.36	5.30	62.45
<i>Escharella immersa</i>	0.67	0.25	4.96	67.41
<i>Patinella verrucaria</i>	0.62	0.20	4.94	72.35
<i>Diplosolen obelia</i>	0.64	0.10	4.89	77.24
<i>Disporella hispida</i>	0.32	0.10	2.39	79.63
<i>Callopora lineata</i>	0.28	0.11	2.38	82.01
<i>Tubulipora phalangea</i>	0.30	0.12	2.37	84.38
<i>Amphiblestrum flemingii</i>	0.32	0.06	2.31	86.69
<i>Escharella klugei</i>	0.18	0.18	2.20	88.90
<i>Crisia eburnea</i>	0.25	0.02	1.96	90.86
<i>Verruca stroemia</i>	0.20	0.00	1.50	92.36
<i>Porella concinna</i>	0.14	0.08	1.16	93.51
<i>Spirobranchus lamarckii</i>	0.12	0.00	0.96	94.47
<i>Tubulipora liliacea</i>	0.08	0.07	0.92	95.40
<i>Cribrilina annulata</i>	0.12	0.04	0.90	96.30
<i>Chorizopora brongniartii</i>	0.07	0.10	0.78	97.08
<i>Hippothoa flagellum</i>	0.09	0.03	0.72	97.80
<i>Balanus crenatus</i>	0.08	0.00	0.52	98.32
<i>Plagioecia sarniensis</i>	0.05	0.00	0.32	98.64
<i>Plagioecia patina</i>	0.04	0.00	0.31	98.95
<i>Fenestulina malusii</i>	0.04	0.00	0.28	99.23
<i>Callopora craticula</i>	0.02	0.02	0.20	99.43
<i>Aeta sica</i>	0.03	0.00	0.17	99.60
<i>Escharella ventricosa</i>	0.02	0.00	0.16	99.76
<i>Aetea truncata</i>	0.02	0.00	0.13	99.89
<i>Crisia aculeata</i>	0.02	0.00	0.11	100.00

Regions 2 & 3

Average dissimilarity = 82.40

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.92	0.87	18.37	18.37
<i>Balanus balanus</i>	2.05	0.15	17.30	35.67
<i>Scrupocellaria scruposa</i>	1.72	0.14	12.98	48.64
<i>Spirorbis tridentatus</i>	1.32	0.60	9.29	57.93

<i>Escharella immersa</i>	0.72	0.25	5.63	63.56
<i>Microporella ciliata</i>	0.62	0.36	4.96	68.52
<i>Serpula sp.</i>	0.57	0.17	4.63	73.14
<i>Patinella verrucaria</i>	0.44	0.20	3.98	77.12
<i>Diplosolen obelia</i>	0.43	0.10	3.27	80.40
<i>Porella concinna</i>	0.40	0.08	3.20	83.60
<i>Escharella klugei</i>	0.19	0.18	2.36	85.95
<i>Disporella hispida</i>	0.22	0.10	1.90	87.86
<i>Crisia eburnea</i>	0.19	0.02	1.43	89.28
<i>Verruca stroemia</i>	0.14	0.00	1.28	90.57
<i>Callopora lineata</i>	0.10	0.11	1.10	91.67
<i>Chorizopora brongniartii</i>	0.11	0.10	1.05	92.72
<i>Tubulipora phalangea</i>	0.07	0.12	1.03	93.75
<i>Balanus crenatus</i>	0.11	0.00	0.92	94.66
<i>Amphiblestrum flemingii</i>	0.09	0.06	0.85	95.51
<i>Tubulipora liliacea</i>	0.06	0.07	0.81	96.31
<i>Spirobranchus lamarckii</i>	0.11	0.00	0.71	97.02
<i>Aeta sica</i>	0.09	0.00	0.64	97.66
<i>Plagioecia sarniensis</i>	0.08	0.00	0.54	98.20
<i>Cribrilina annulata</i>	0.04	0.04	0.43	98.63
<i>Hippothoa flagellum</i>	0.04	0.03	0.39	99.03
<i>Escharella ventricosa</i>	0.04	0.00	0.30	99.33
<i>Fenestrulina malusii</i>	0.04	0.00	0.28	99.61
<i>Celleporella hyalina</i>	0.02	0.00	0.14	99.75
<i>Crisia aculeata</i>	0.02	0.00	0.13	99.88
<i>Callopora craticula</i>	0.00	0.02	0.12	100.00

Regions 1 & 4

Average dissimilarity = 66.33

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.75	2.07	13.92	13.92
<i>Balanus balanus</i>	1.72	0.52	12.48	26.41
<i>Scrupocellaria scruposa</i>	1.61	0.55	11.63	38.04
<i>Spirorbis tridentatus</i>	1.21	1.11	9.02	47.06
<i>Microporella ciliata</i>	0.73	0.59	5.92	52.98
<i>Escharella immersa</i>	0.67	0.59	5.86	58.84
<i>Serpula sp.</i>	0.67	0.46	5.68	64.53

<i>Diplosolen obelia</i>	0.64	0.34	5.10	69.62
<i>Patinella verrucaria</i>	0.62	0.32	4.97	74.59
<i>Callopora lineata</i>	0.28	0.18	2.81	77.40
<i>Tubulipora phalangea</i>	0.30	0.20	2.67	80.08
<i>Disporella hispida</i>	0.32	0.06	2.37	82.44
<i>Crisia eburnea</i>	0.25	0.11	2.31	84.75
<i>Amphiblestrum flemingii</i>	0.32	0.04	2.29	87.04
<i>Escharella klugei</i>	0.18	0.09	1.67	88.71
<i>Verruca stroemia</i>	0.20	0.02	1.57	90.28
<i>Porella concinna</i>	0.14	0.12	1.48	91.76
<i>Spirobranchus lamareckii</i>	0.12	0.02	1.05	92.81
<i>Balanus crenatus</i>	0.08	0.09	1.04	93.85
<i>Cribilina annulata</i>	0.12	0.04	0.98	94.83
<i>Chorizopora brongniartii</i>	0.07	0.11	0.97	95.80
<i>Hippothoa flagellum</i>	0.09	0.05	0.88	96.68
<i>Tubulipora liliacea</i>	0.08	0.04	0.74	97.41
<i>Fenestulina malusii</i>	0.04	0.04	0.55	97.96
<i>Plagioecia sarniensis</i>	0.05	0.02	0.44	98.39
<i>Aeta sica</i>	0.03	0.04	0.39	98.78
<i>Plagioecia patina</i>	0.04	0.00	0.31	99.09
<i>Tubulipora plumosa</i>	0.00	0.05	0.29	99.38
<i>Escharella ventricosa</i>	0.02	0.00	0.16	99.54
<i>Aetea truncata</i>	0.02	0.00	0.13	99.67
<i>Crisia aculeata</i>	0.02	0.00	0.12	99.79
<i>Electra pilosa</i>	0.00	0.02	0.11	99.91
<i>Callopora craticula</i>	0.02	0.00	0.09	100.00

Regions 2 & 4

Average dissimilarity = 64.79

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	2.05	0.52	15.50	15.50
<i>Spirobranchus triqueter</i>	2.92	2.07	14.47	29.96
<i>Scrupocellaria scruposa</i>	1.72	0.55	12.23	42.19
<i>Spirorbis tridentatus</i>	1.32	1.11	9.27	51.46
<i>Escharella immersa</i>	0.72	0.59	6.35	57.81
<i>Microporella ciliata</i>	0.62	0.59	5.72	63.53
<i>Serpula sp.</i>	0.57	0.46	5.40	68.93

<i>Patinella verrucaria</i>	0.44	0.32	4.31	73.24
<i>Diplosolen obelia</i>	0.43	0.34	1.14	77.40
<i>Porella concinna</i>	0.40	0.12	3.38	80.77
<i>Disporella hispida</i>	0.22	0.06	1.88	82.65
<i>Escharella klugei</i>	0.19	0.09	1.88	84.53
<i>Crisia eburnea</i>	0.19	0.11	1.87	86.40
<i>Callopora lineata</i>	0.10	0.18	1.69	88.09
<i>Tubulipora phalangea</i>	0.07	0.20	1.49	89.58
<i>Balanus crenatus</i>	0.11	0.09	1.46	91.04
<i>Verruca stroemia</i>	0.14	0.02	1.36	92.40
<i>Chorizopora brongniartii</i>	0.11	0.11	1.25	93.65
<i>Aeta sica</i>	0.09	0.04	0.85	94.50
<i>Spirobranchus lamarckii</i>	0.11	0.02	0.85	95.34
<i>Amphiblestrum flemingii</i>	0.09	0.04	0.75	96.09
<i>Plagioecia sarniensis</i>	0.08	0.02	0.67	96.76
<i>Tubulipora liliacea</i>	0.06	0.04	0.61	97.37
<i>Hippothoa flagellum</i>	0.04	0.05	0.57	97.94
<i>Fenestulina malusii</i>	0.04	0.04	0.55	98.49
<i>Cribrilina annulata</i>	0.04	0.04	0.50	98.99
<i>Escharella ventricosa</i>	0.04	0.00	0.31	99.30
<i>Tubulipora plumosa</i>	0.00	0.05	0.30	99.60
<i>Celleporella hyalina</i>	0.02	0.00	0.14	99.74
<i>Crisia aculeata</i>	0.02	0.00	0.14	99.88
<i>Electra pilosa</i>	0.00	0.02	0.12	100.00

Regions 3 & 4

Average dissimilarity = 83.44

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.87	2.07	22.88	22.88
<i>Spirorbis tridentatus</i>	0.60	1.11	13.42	36.29
<i>Serpula sp.</i>	0.17	0.46	8.29	44.55
<i>Microporella ciliata</i>	0.36	0.59	7.57	52.16
<i>Escharella immersa</i>	0.25	0.59	7.07	59.23
<i>Balanus balanus</i>	0.15	0.52	7.03	66.27
<i>Scrupocellaria scruposa</i>	0.14	0.55	6.08	72.35
<i>Diplosolen obelia</i>	0.10	0.34	4.85	77.19
<i>Patinella verrucaria</i>	0.20	0.32	3.78	80.98

<i>Escharella klugei</i>	0.18	0.09	2.64	83.62
<i>Callopora lineata</i>	0.11	0.18	2.44	86.06
<i>Tubulipora phalangea</i>	0.12	0.20	2.37	88.43
<i>Porella concinna</i>	0.08	0.12	2.00	90.42
<i>Disporella hispida</i>	0.10	0.06	1.64	92.06
<i>Chorizopora brongniartii</i>	0.10	0.11	1.34	93.40
<i>Crisia eburnea</i>	0.02	0.11	1.05	94.45
<i>Tubulipora liliacea</i>	0.07	0.04	0.93	95.39
<i>Amphiblestrum flemingii</i>	0.06	0.04	0.82	96.21
<i>Balanus crenatus</i>	0.00	0.09	0.75	96.96
<i>Cribilina annulata</i>	0.04	0.04	0.58	97.54
<i>Hippothoa flagellum</i>	0.03	0.05	0.54	98.09
<i>Fenestulina malusii</i>	0.00	0.04	0.43	98.52
<i>Tubulipora plumosa</i>	0.00	0.05	0.43	98.95
<i>Aeta sica</i>	0.00	0.04	0.27	99.22
<i>Verruca stroemia</i>	0.00	0.02	0.17	99.39
<i>Callopora craticula</i>	0.02	0.00	0.17	99.56
<i>Spirobranchus lamarckii</i>	0.00	0.02	0.15	99.71
<i>Plagioecia sarniensis</i>	0.00	0.02	0.14	99.86
<i>Electra pilosa</i>	0.00	0.02	0.14	100.00

Appendix D11. Output: Loch Creran SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1

Average similarity: 63.66

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.09	63.26	2.52	99.38	99.38
<i>Callopora lineata</i>	0.11	0.23	0.09	0.37	99.75
<i>Disporella hispida</i>	0.06	0.09	0.05	0.14	99.89
<i>Patinella verrucaria</i>	0.06	0.07	0.05	0.11	100.00

Region 2

Average similarity: 39.29

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.98	39.25	0.93	99.88	99.99
<i>Disporella hispida</i>	0.04	0.05	0.03	0.12	100.00

Region 3

Average similarity: 19.43

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.56	19.19	0.54	98.78	98.78
<i>Callopora lineata</i>	0.05	0.24	0.06	1.22	100.00

Region 4

Average similarity: 26.80

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	0.70	26.80	0.70	100.00	100.00

Appendix D12. Output: Loch Creran outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 54.23

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.09	0.98	84.21	84.21
<i>Disporella hispida</i>	0.06	0.04	5.05	89.26
<i>Callopora lineata</i>	0.11	0.00	4.75	94.01
<i>Patinella verrucaria</i>	0.06	0.00	2.61	96.62
<i>Balanus balanus</i>	0.03	0.00	1.62	98.24
<i>Tubulipora phalangea</i>	0.02	0.00	1.05	99.28
<i>Escharella immersa</i>	0.02	0.00	0.72	100.00

Regions 1 & 3

Average dissimilarity = 72.56

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.09	0.56	85.58	85.58
<i>Callopora lineata</i>	0.11	0.06	6.09	91.66
<i>Disporella hispida</i>	0.06	0.02	3.37	95.03
<i>Patinella verrucaria</i>	0.06	0.00	2.17	97.20
<i>Balanus balanus</i>	0.03	0.00	1.34	98.54
<i>Tubulipora phalangea</i>	0.02	0.00	0.88	99.42
<i>Escharella immersa</i>	0.02	0.00	0.58	100.00

Regions 2 & 3

Average dissimilarity = 73.13

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.98	0.56	90.57	90.57
<i>Callopora lineata</i>	0.00	0.06	4.91	95.48
<i>Disporella hispida</i>	0.04	0.02	4.52	100.00

Regions 1 & 4

Average dissimilarity = 65.65

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.09	0.70	85.23	85.23
<i>Callopora lineata</i>	0.11	0.02	4.72	89.94
<i>Disporella hispida</i>	0.06	0.02	3.46	93.40
<i>Patinella verrucaria</i>	0.06	0.02	2.86	96.27
<i>Balanus balanus</i>	0.03	0.00	1.43	97.70

Regions 2 & 4

Average dissimilarity = 67.41

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.98	0.70	92.65	92.65
<i>Disporella hispida</i>	0.04	0.02	4.27	96.92
<i>Escharella immersa</i>	0.00	0.02	1.26	98.18
<i>Patinella verrucaria</i>	0.00	0.02	0.91	99.09
<i>Callopora lineata</i>	0.00	0.02	0.91	100.00

Regions 3 & 4

Average dissimilarity = 76.56

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	0.56	0.70	88.28	88.28
<i>Callopora lineata</i>	0.06	0.02	6.90	95.18
<i>Disporella hispida</i>	0.02	0.02	2.37	97.54
<i>Escharella immersa</i>	0.00	0.02	1.44	98.99

<i>Patinella verrucaria</i>	0.00	0.02	1.01	100.00
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Appendix D13. Output: Noss Head SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1

Average similarity: 33.79

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Diplosolen obelia</i>	1.74	6.18	0.79	18.29	18.29
<i>Membraniporella nitida</i>	1.52	4.98	0.74	14.73	33.01
<i>Spirorbis tridentatus</i>	2.20	4.52	0.71	13.37	46.38
<i>Escharoides coccinea</i>	1.64	4.13	0.66	12.21	58.59
<i>Escharella immersa</i>	1.32	3.76	0.78	11.14	69.73
<i>Spirobranchus triqueter</i>	1.44	3.59	0.69	10.63	80.36
<i>Schizomavella linearis</i>	0.62	1.62	0.46	4.80	85.16
<i>Amphiblestrum flemingii</i>	0.68	1.13	0.37	3.35	88.51
<i>Patinella verrucaria</i>	0.62	0.91	0.32	2.70	91.21
<i>Tubulipora lobifera</i>	0.54	0.80	0.32	2.36	93.56
<i>Verruca stroemia</i>	0.60	0.78	0.36	2.32	95.89
<i>Smittoidea reticulata</i>	0.48	0.57	0.31	2.67	97.56
<i>Celleporella hyalina</i>	0.34	0.20	0.14	0.61	98.17
<i>Microporella ciliata</i>	0.20	0.18	0.17	0.52	98.69
<i>Serpula sp.</i>	0.18	0.14	0.15	0.41	99.10
<i>Tubulipora phalangea</i>	0.20	0.14	0.15	0.40	99.50
<i>Tubulipora liliacea</i>	0.16	0.05	0.09	0.16	99.66
<i>Cellepora pumicosa</i>	0.10	0.04	0.07	0.11	99.77
<i>Disporella hispida</i>	0.10	0.03	0.07	0.09	99.86
<i>Balanus balanus</i>	0.06	0.02	0.05	0.05	99.90
<i>Fenestrulina malusii</i>	0.10	0.01	0.05	0.04	99.94
<i>Plagioecia sarniensis</i>	0.04	0.01	0.03	0.03	99.97
<i>Plagioecia patina</i>	0.04	0.01	0.03	0.02	99.99
<i>Callopora lineata</i>	0.04	0.00	0.03	0.01	100.00

Region 2
Average similarity: 33.24

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Diplosolen obelia</i>	1.98	7.32	0.85	22.02	22.02
<i>Spirobranchus triqueter</i>	1.66	5.42	0.78	16.31	38.33
<i>Escharella immersa</i>	1.40	4.29	0.73	12.89	51.22
<i>Membraniporella nitida</i>	1.56	4.23	0.63	12.72	63.94
<i>Spirorbis tridentatus</i>	1.76	3.81	0.59	11.46	75.40
<i>Escharoides coccinea</i>	1.02	2.92	0.55	8.79	84.19
<i>Patinella verrucaria</i>	0.74	1.55	0.46	4.67	88.86
<i>Tubulipora lobifera</i>	0.48	0.94	0.32	2.84	91.70
<i>Schizomavella linearis</i>	0.38	0.49	0.25	1.48	93.18
<i>Microporella ciliata</i>	0.32	0.43	0.25	1.31	94.48
<i>Verruca stroemia</i>	0.36	0.41	0.24	1.23	95.71
<i>Tubulipora phalangea</i>	0.32	0.39	0.23	1.17	96.88
<i>Smittoidea reticulata</i>	0.24	0.29	0.18	0.86	97.74
<i>Amphiblestrum flemingii</i>	0.26	0.26	0.21	0.79	98.53
<i>Celleporella hyalina</i>	0.28	0.20	0.16	0.60	99.12
<i>Tubulipora liliacea</i>	0.18	0.12	0.13	0.37	99.50
<i>Cellepora pumicosa</i>	0.12	0.05	0.09	0.16	99.65
<i>Plagioecia patina</i>	0.12	0.05	0.07	0.15	99.81
<i>Plagioecia sarniensis</i>	0.14	0.04	0.07	0.11	99.91
<i>Balanus balanus</i>	0.06	0.02	0.05	0.06	99.97
<i>Serpula sp.</i>	0.04	0.00	0.03	0.01	99.99
<i>Spirobranchus lamarckii</i>	0.04	0.00	0.03	0.01	100.00

Region 3
Average similarity: 19.01

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirorbis tridentatus</i>	1.66	4.90	0.55	25.79	25.79
<i>Escharoides coccinea</i>	0.90	3.51	0.47	18.49	44.27
<i>Escharella immersa</i>	0.86	3.12	0.49	16.40	60.67
<i>Schizomavella linearis</i>	0.56	1.74	0.41	9.17	69.84

<i>Patinella verrucaria</i>	0.54	1.26	0.30	6.63	76.47
<i>Diplosolen obelia</i>	0.36	0.90	0.26	4.71	81.18
<i>Membraniporella nitida</i>	0.40	0.88	0.25	4.65	85.82
<i>Spirobranchus triqueter</i>	0.36	0.56	0.22	2.97	88.79
<i>Microporella ciliata</i>	0.20	0.45	0.15	2.37	91.16
<i>Smittoidea reticulata</i>	0.24	0.39	0.18	2.03	93.18
<i>Fenestrulina malusii</i>	0.26	0.36	0.21	1.91	95.09
<i>Tubulipora phalangea</i>	0.22	0.28	0.14	1.47	96.56
<i>Tubulipora lobifera</i>	0.20	0.25	0.14	1.32	97.88
<i>Amphiblestrum flemingii</i>	0.32	0.21	0.13	1.08	98.97
<i>Serpula sp.</i>	0.24	0.06	0.09	0.31	99.28
<i>Cellepora pumicosa</i>	0.08	0.05	0.07	0.27	99.55
<i>Tubulipora liliacea</i>	0.08	0.05	0.07	0.27	99.82
<i>Verruca stroemia</i>	0.10	0.03	0.07	0.18	100.00

Region 4

Average similarity: 30.47

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirorbis tridentatus</i>	2.88	6.85	0.69	22.48	22.48
<i>Escharella immersa</i>	1.78	6.02	0.71	19.76	42.24
<i>Spirobranchus triqueter</i>	1.10	4.00	0.63	13.12	55.36
<i>Escharoides coccinea</i>	1.06	3.90	0.63	12.80	68.16
<i>Diplosolen obelia</i>	0.88	3.52	0.54	11.56	79.71
<i>Membraniporella nitida</i>	0.66	1.66	0.49	5.45	85.16
<i>Patinella verrucaria</i>	0.60	1.63	0.37	5.36	90.52
<i>Schizomavella linearis</i>	0.50	1.00	0.31	3.29	93.81
<i>Tubulipora phalangea</i>	0.24	0.45	0.19	1.48	95.29
<i>Smittoidea reticulata</i>	0.32	0.36	0.20	1.19	96.48
<i>Amphiblestrum flemingii</i>	0.28	0.32	0.23	1.04	97.52
<i>Tubulipora lobifera</i>	0.26	0.28	0.17	0.91	98.43
<i>Microporella ciliata</i>	0.18	0.18	0.15	0.57	99.00
<i>Verruca stroemia</i>	0.18	0.15	0.14	0.48	99.48

<i>Cellepora pumicosa</i>	0.14	0.05	0.09	0.17	99.65
<i>Fenestrulina malusii</i>	0.08	0.05	0.06	0.16	99.81
<i>Tubulipora liliacea</i>	0.06	0.03	0.05	0.09	99.90
<i>Plagioecia sarniensis</i>	0.12	0.02	0.05	0.05	99.95
<i>Hippothoa flagellum</i>	0.06	0.01	0.05	0.03	99.98
<i>Serpula sp.</i>	0.14	0.01	0.03	0.02	100.00

Appendix D14. Output: Noss Head outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 66.43

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Spirorbis tridentatus</i>	2.20	1.76	12.63	12.63
<i>Diplosolen obelia</i>	1.74	1.98	10.79	23.41
<i>Membraniporella nitida</i>	1.52	1.56	9.66	33.07
<i>Spirobranchus triqueter</i>	1.44	1.66	9.45	42.52
<i>Escharoides coccinea</i>	1.64	1.02	9.16	51.68
<i>Escharella immersa</i>	1.32	1.40	8.48	60.16
<i>Patinella verrucaria</i>	0.62	0.74	5.18	65.34
<i>Schizomavella linearis</i>	0.62	0.38	4.20	69.54
<i>Tubulipora lobifera</i>	0.54	0.48	4.11	73.64
<i>Amphiblestrum flemingii</i>	0.68	0.26	3.91	77.55
<i>Verruca stroemia</i>	0.60	0.36	3.80	81.35
<i>Smittoidea reticulata</i>	0.48	0.24	3.08	84.43
<i>Celleporella hyalina</i>	0.34	0.28	2.88	87.31
<i>Microporella ciliata</i>	0.20	0.32	2.27	89.58
<i>Tubulipora phalangea</i>	0.20	0.32	2.25	91.83
<i>Tubulipora liliacea</i>	0.16	0.18	1.62	93.45
<i>Cellepora pumicosa</i>	0.10	0.12	1.11	94.56
<i>Serpula sp.</i>	0.18	0.04	1.06	95.62
<i>Plagioecia patina</i>	0.04	0.12	0.94	96.56
<i>Plagioecia sarniensis</i>	0.04	0.14	0.93	97.49
<i>Balanus balanus</i>	0.06	0.06	0.64	98.13
<i>Disporella hispida</i>	0.10	0.02	0.62	98.76
<i>Fenestrulina malusii</i>	0.10	0.00	0.41	99.16

<i>Callopora lineata</i>	0.04	0.02	0.34	99.50
<i>Spirobranchus lamarckii</i>	0.00	0.04	0.19	99.70
<i>Escharella variolosa</i>	0.00	0.02	0.13	99.82
<i>Scrupocellaria scruposa</i>	0.02	0.00	0.11	99.93
<i>Electra pilosa</i>	0.02	0.00	0.07	100.00

Regions 1 & 3

Average dissimilarity = 77.43

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirorbis tridentatus</i>	2.20	1.66	13.33	13.33
<i>Diplosolen obelia</i>	1.74	0.36	10.88	24.21
<i>Escharoides coccinea</i>	1.64	0.90	10.10	34.30
<i>Membraniporella nitida</i>	1.52	0.40	9.33	43.63
<i>Escharella immersa</i>	1.32	0.86	8.38	52.02
<i>Spirobranchus triqueter</i>	1.44	0.36	8.28	60.30
<i>Patinella verrucaria</i>	0.62	0.54	5.22	65.52
<i>Schizomavella linearis</i>	0.62	0.56	4.93	70.45
<i>Amphiblestrum flemingii</i>	0.68	0.32	4.80	75.25
<i>Tubulipora lobifera</i>	0.54	0.20	3.56	78.81
<i>Verruca stroemia</i>	0.60	0.10	3.43	82.25
<i>Smittoidea reticulata</i>	0.48	0.24	3.20	85.45
<i>Microporella ciliata</i>	0.20	0.20	2.14	87.59
<i>Tubulipora phalangea</i>	0.20	0.22	2.07	89.66
<i>Celleporella hyalina</i>	0.34	0.00	1.99	91.64
<i>Serpula sp.</i>	0.18	0.24	1.83	93.48
<i>Fenestrulina malusii</i>	0.10	0.26	1.58	95.06
<i>Tubulipora liliacea</i>	0.16	0.08	1.27	96.33
<i>Cellepora pumicosa</i>	0.10	0.08	1.08	97.41
<i>Disporella hispida</i>	0.10	0.00	0.61	98.02
<i>Spirobranchus lamarckii</i>	0.00	0.06	0.46	98.48
<i>Balanus balanus</i>	0.06	0.00	0.38	98.86
<i>Plagioecia sarniensis</i>	0.04	0.00	0.35	99.21
<i>Plagioecia patina</i>	0.04	0.00	0.29	99.50
<i>Callopora lineata</i>	0.04	0.00	0.23	99.73
<i>Scrupocellaria scruposa</i>	0.02	0.00	0.12	99.85
<i>Escharella variolosa</i>	0.00	0.02	0.09	99.94
<i>Electra pilosa</i>	0.02	0.00	0.06	100.00

Regions 2 & 3

Average dissimilarity = 78.42

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Spirorbis tridentatus</i>	1.76	1.66	13.19	13.19
<i>Diplosolen obelia</i>	1.98	0.36	12.54	25.73
<i>Spirobranchus triqueter</i>	1.66	0.36	10.08	35.81
<i>Membraniporella nitida</i>	1.56	0.40	9.59	45.40
<i>Escharella immersa</i>	1.40	0.86	9.23	54.64
<i>Escharoides coccinea</i>	1.02	0.90	8.22	62.86
<i>Patinella verrucaria</i>	0.74	0.54	5.77	68.63
<i>Schizomavella linearis</i>	0.38	0.56	4.16	72.79
<i>Tubulipora lobifera</i>	0.48	0.20	3.74	76.53
<i>Tubulipora phalangea</i>	0.32	0.22	2.83	79.36
<i>Microporella ciliata</i>	0.32	0.20	2.77	82.13
<i>Amphiblestrum flemingii</i>	0.26	0.32	2.63	84.76
<i>Verruca stroemia</i>	0.36	0.10	2.63	87.39
<i>Smittoidea reticulata</i>	0.24	0.24	2.59	89.98
<i>Celleporella hyalina</i>	0.28	0.00	1.66	91.64
<i>Tubulipora liliacea</i>	0.18	0.08	1.48	93.12
<i>Fenestulina malusii</i>	0.00	0.26	1.30	94.42
<i>Serpula</i> sp.	0.04	0.24	1.15	95.57
<i>Cellepora pumicosa</i>	0.12	0.08	1.09	96.66
<i>Plagioecia patina</i>	0.12	0.00	0.90	97.56
<i>Plagioecia sarniensis</i>	0.14	0.00	0.78	98.33
<i>Spirobranchus lamarckii</i>	0.04	0.06	0.70	99.03
<i>Balanus balanus</i>	0.06	0.00	0.43	99.46
<i>Escharella variolosa</i>	0.02	0.02	0.25	99.71
<i>Callopora lineata</i>	0.02	0.00	0.19	99.90
<i>Disporella hispida</i>	0.02	0.00	0.10	100.00

Regions 1 & 4

Average dissimilarity = 69.33

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirorbis tridentatus</i>	2.20	2.88	15.85	15.85
<i>Escharella immersa</i>	1.32	1.78	9.96	25.81
<i>Diplosolen obelia</i>	1.74	0.88	9.43	35.24

<i>Escharoides coccinea</i>	1.64	1.06	9.38	44.62
<i>Spirobranchus triqueter</i>	1.44	1.10	8.46	53.08
<i>Membraniporella nitida</i>	1.52	0.66	8.42	61.50
<i>Patinella verrucaria</i>	0.62	0.60	5.16	66.66
<i>Schizomavella linearis</i>	0.62	0.50	4.59	71.25
<i>Amphiblestrum flemingii</i>	0.68	0.28	4.10	75.35
<i>Tubulipora lobifera</i>	0.54	0.26	3.67	79.02
<i>Smittoidea reticulata</i>	0.48	0.32	3.47	82.49
<i>Verruca stroemia</i>	0.60	0.18	3.42	85.91
<i>Tubulipora phalangea</i>	0.20	0.24	2.30	88.21
<i>Celleporella hyalina</i>	0.34	0.02	1.92	90.13
<i>Microporella ciliata</i>	0.20	0.18	1.82	91.95
<i>Serpula</i> sp.	0.18	0.14	1.51	93.45
<i>Cellepora pumicosa</i>	0.10	0.14	1.22	94.67
<i>Tubulipora liliacea</i>	0.16	0.06	1.17	95.83
<i>Fenestulina malusii</i>	0.10	0.08	0.88	96.71
<i>Plagioecia sarniensis</i>	0.04	0.12	0.82	97.53
<i>Disporella hispida</i>	0.10	0.02	0.68	98.21
<i>Plagioecia patina</i>	0.04	0.06	0.62	98.84
<i>Balanus balanus</i>	0.06	0.00	0.35	99.19
<i>Callopora lineata</i>	0.04	0.02	0.35	99.54
<i>Hippothoa flagellum</i>	0.00	0.06	0.22	99.75
<i>Scrupocellaria scruposa</i>	0.02	0.00	0.12	99.87
<i>Electra pilosa</i>	0.02	0.00	0.07	99.94
<i>Escharella variolosa</i>	0.00	0.02	0.06	100.00

Regions 2 & 4

Average dissimilarity = 69.42

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirorbis tridentatus</i>	1.76	2.88	16.20	16.20
<i>Diplosolen obelia</i>	1.98	0.88	10.88	27.09
<i>Escharella immersa</i>	1.40	1.78	10.65	37.74
<i>Spirobranchus triqueter</i>	1.66	1.10	9.49	47.23
<i>Membraniporella nitida</i>	1.56	0.66	9.07	56.30
<i>Escharoides coccinea</i>	1.02	1.06	7.78	64.08
<i>Patinella verrucaria</i>	0.74	0.60	5.64	69.72
<i>Schizomavella linearis</i>	0.38	0.50	3.90	73.63

<i>Tubulipora lobifera</i>	0.48	0.26	3.78	77.41
<i>Tubulipora phalangea</i>	0.32	0.24	2.97	80.38
<i>Smittoidea reticulata</i>	0.24	0.32	2.89	83.26
<i>Verruca stroemia</i>	0.36	0.18	2.48	85.75
<i>Microporella ciliata</i>	0.32	0.18	2.42	88.16
<i>Amphiblestrum flemingii</i>	0.26	0.28	2.23	90.40
<i>Celleporella hyalina</i>	0.28	0.02	1.62	92.02
<i>Tubulipora liliacea</i>	0.18	0.06	1.36	93.38
<i>Cellepora pumicosa</i>	0.12	0.14	1.27	94.65
<i>Plagioecia sarniensis</i>	0.14	0.12	1.24	95.89
<i>Plagioecia patina</i>	0.12	0.06	1.18	97.07
<i>Serpula sp.</i>	0.04	0.14	0.82	97.89
<i>Fenestulina malusii</i>	0.00	0.08	0.53	98.42
<i>Balanus balanus</i>	0.06	0.00	0.39	98.81
<i>Callopora lineata</i>	0.02	0.02	0.31	99.12
<i>Disporella hispida</i>	0.02	0.02	0.23	99.36
<i>Hippothoa flagellum</i>	0.00	0.06	0.22	99.58
<i>Spirobranchus lamarckii</i>	0.04	0.00	0.21	99.79
<i>Escharella variolosa</i>	0.02	0.02	0.21	100.00

Regions 3 & 4

Average dissimilarity = 76.55

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Spirorbis tridentatus</i>	1.66	2.88	19.02	19.02
<i>Escharella immersa</i>	0.86	1.78	12.64	31.66
<i>Escharoides coccinea</i>	0.90	1.06	9.23	40.89
<i>Spirobranchus triqueter</i>	0.36	1.10	8.46	49.35
<i>Diplosolen obelia</i>	0.36	0.88	7.64	56.99
<i>Patinella verrucaria</i>	0.54	0.60	6.72	63.71
<i>Membraniporella nitida</i>	0.40	0.66	5.46	69.17
<i>Schizomavella linearis</i>	0.56	0.50	5.33	74.50
<i>Tubulipora phalangea</i>	0.22	0.24	3.54	78.04
<i>Smittoidea reticulata</i>	0.24	0.32	3.29	81.33
<i>Amphiblestrum flemingii</i>	0.32	0.28	2.99	84.33
<i>Tubulipora lobifera</i>	0.20	0.26	2.90	87.22
<i>Microporella ciliata</i>	0.20	0.18	2.56	89.78
<i>Fenestulina malusii</i>	0.26	0.08	2.04	91.82

<i>Serpula</i> sp.	0.24	0.14	1.73	93.55
<i>Verruca stroemia</i>	0.10	0.18	1.51	95.07
<i>Cellepore pumicosa</i>	0.08	0.14	1.29	96.35
<i>Tubulipora liliacea</i>	0.08	0.06	1.05	97.40
<i>Plagioecia sarniensis</i>	0.00	0.12	0.63	98.30
<i>Spirobranchus lamarckii</i>	0.06	0.00	0.60	98.63
<i>Plagioecia patina</i>	0.00	0.06	0.50	99.13
<i>Hippothoa flagellum</i>	0.00	0.06	0.24	99.37
<i>Callopora lineata</i>	0.00	0.02	0.21	99.58
<i>Disporella hispida</i>	0.00	0.02	0.18	99.76
<i>Escharella variolosa</i>	0.02	0.02	0.17	99.93
<i>Celleporella hyalina</i>	0.00	0.02	0.07	100.00

Appendix D15. Output: Dornoch Firth SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell region

Region 1

Average similarity: 33.70

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Balanus balanus</i>	4.88	21.40	1.11	63.49	63.49
<i>Conopeum reticulum</i>	1.10	4.15	0.58	12.33	75.82
<i>Balanus crenatus</i>	2.62	3.52	0.47	10.45	86.27
<i>Callopora lineata</i>	0.60	1.17	0.36	3.46	89.73
<i>Electra pilosa</i>	0.46	1.16	0.30	3.43	93.16
<i>Spirobranchus triqueter</i>	0.50	0.96	0.25	2.84	95.99
<i>Celleporella hyalina</i>	0.84	0.93	0.31	2.77	98.76
<i>Escharella immersa</i>	0.20	0.26	0.13	0.78	99.54
<i>Verruca stroemia</i>	0.10	0.08	0.09	0.22	99.76
<i>Cribrilina punctata</i>	0.14	0.08	0.10	0.22	99.98
<i>Callopora craticula</i>	0.04	0.01	0.03	0.02	100.00

Region 2

Average similarity: 33.71

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Balanus balanus</i>	3.32	17.31	0.89	51.34	51.34
<i>Balanus crenatus</i>	2.32	7.09	0.54	21.03	72.37

<i>Conopeum reticulum</i>	0.98	6.48	0.70	19.22	91.59
<i>Celleporella hyalina</i>	0.94	1.28	0.23	3.79	95.38
<i>Callopora lineata</i>	0.42	0.94	0.28	2.79	98.16
<i>Spirobranchus triqueter</i>	0.26	0.33	0.15	0.98	99.15
<i>Electra pilosa</i>	0.20	0.13	0.10	0.38	99.53
<i>Callopora craticula</i>	0.10	0.07	0.08	0.20	99.73
<i>Verruca stroemia</i>	0.08	0.04	0.05	0.13	99.86
<i>Microporella ciliata</i>	0.06	0.04	0.05	0.12	99.98
<i>Cribrilina punctata</i>	0.04	0.01	0.03	0.02	100.00

Region 3

Average similarity: 11.55

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Conopeum reticulum</i>	0.58	8.77	0.45	75.89	75.89
<i>Balanus balanus</i>	0.78	1.10	0.18	9.49	85.39
<i>Spirobranchus triqueter</i>	0.30	0.99	0.17	8.53	93.92
<i>Cribrilina punctata</i>	0.22	0.62	0.12	5.40	99.32
<i>Escharella immersa</i>	0.04	0.03	0.03	0.24	99.57
<i>Callopora lineata</i>	0.06	0.02	0.05	0.21	99.78
<i>Electra pilosa</i>	0.10	0.01	0.03	0.09	99.87
<i>Celleporella hyalina</i>	0.16	0.01	0.03	0.09	99.96
<i>Balanus crenatus</i>	0.72	0.01	0.03	0.04	100.00

Region 4

Average similarity: 22.33

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Conopeum reticulum</i>	1.06	8.54	0.58	38.24	38.24
<i>Balanus crenatus</i>	1.82	4.60	0.46	20.61	58.86
<i>Balanus balanus</i>	1.30	4.25	0.45	19.06	77.91
<i>Spirobranchus triqueter</i>	1.06	3.74	0.35	16.74	94.65
<i>Celleporella hyalina</i>	0.48	0.55	0.17	2.48	97.13
<i>Electra pilosa</i>	0.18	0.21	0.12	0.95	98.08
<i>Cribrilina punctata</i>	0.14	0.21	0.13	0.94	99.02

<i>Escharella immersa</i>	0.10	0.15	0.09	0.68	99.70
<i>Callopora lineata</i>	0.10	0.05	0.06	0.21	99.91
<i>Verruca stroemia</i>	0.04	0.02	0.03	0.09	100.00

Appendix D16. Output: Dornoch Firth outcomes showing similarity/dissimilarity of epifaunal community between shell regions

Regions 1 & 2

Average dissimilarity = 67.19

Species	Shell region 1 Av.Abund	Shell region 2 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	4.88	3.32	33.66	33.66
<i>Balanus crenatus</i>	2.62	2.32	22.66	56.32
<i>Conopeum reticulum</i>	1.10	0.98	10.91	67.24
<i>Celleporella hyalina</i>	0.84	0.94	9.84	77.08
<i>Callopora lineata</i>	0.60	0.42	5.86	82.94
<i>Spirobranchus triqueter</i>	0.50	0.26	5.57	88.51
<i>Electra pilosa</i>	0.46	0.20	4.60	93.11
<i>Escharella immersa</i>	0.20	0.02	2.14	95.25
<i>Verruca stroemia</i>	0.10	0.08	1.81	97.06
<i>Cribrilina punctata</i>	0.14	0.04	1.16	98.22
<i>Callopora craticula</i>	0.04	0.10	1.12	99.34
<i>Microporella ciliata</i>	0.00	0.06	0.66	100.00

Regions 1 & 3

Average dissimilarity = 88.73

Species	Shell region 1 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	4.88	0.78	40.47	40.47
<i>Balanus crenatus</i>	2.62	0.72	15.23	55.70
<i>Conopeum reticulum</i>	1.10	0.58	12.89	68.59
<i>Spirobranchus triqueter</i>	0.50	0.30	7.48	76.07
<i>Celleporella hyalina</i>	0.84	0.16	5.72	81.79
<i>Electra pilosa</i>	0.46	0.10	5.27	87.06
<i>Callopora lineata</i>	0.60	0.06	4.96	92.02
<i>Escharella immersa</i>	0.20	0.04	3.12	95.14
<i>Cribrilina punctata</i>	0.14	0.22	2.92	98.06

<i>Verruca stroemia</i>	0.10	0.00	0.94	99.00
<i>Callopora craticula</i>	0.04	0.02	0.71	99.72
<i>Microporella ciliata</i>	0.00	0.02	0.28	100.00

Regions 2 & 3

Average dissimilarity = 88.05

Species	Shell region 2 Av.Abund	Shell region 3 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	3.32	0.78	35.82	35.82
<i>Balanus crenatus</i>	2.32	0.72	23.20	59.02
<i>Conopeum reticulum</i>	0.98	0.58	12.73	71.75
<i>Celleporella hyalina</i>	0.94	0.16	8.89	80.65
<i>Spirobranchus triqueter</i>	0.26	0.30	5.39	86.03
<i>Callopora lineata</i>	0.42	0.06	4.47	90.51
<i>Electra pilosa</i>	0.20	0.10	2.21	92.71
<i>Cribilina punctata</i>	0.04	0.22	2.16	94.87
<i>Verruca stroemia</i>	0.08	0.00	2.00	96.87
<i>Microporella ciliata</i>	0.06	0.02	1.18	98.06
<i>Callopora craticula</i>	0.10	0.02	1.16	99.22
<i>Escharella immersa</i>	0.02	0.04	0.78	100.00

Regions 1 & 4

Average dissimilarity = 77.90

Species	Shell region 1 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	4.88	1.30	34.54	34.54
<i>Balanus crenatus</i>	2.62	1.82	18.25	52.79
<i>Conopeum reticulum</i>	1.10	1.06	12.62	65.41
<i>Spirobranchus triqueter</i>	0.50	1.06	11.29	76.70
<i>Celleporella hyalina</i>	0.84	0.48	7.02	83.72
<i>Electra pilosa</i>	0.46	0.18	4.75	88.47
<i>Callopora lineata</i>	0.60	0.10	4.61	93.08
<i>Escharella immersa</i>	0.20	0.10	2.96	96.04
<i>Cribilina punctata</i>	0.14	0.14	1.89	97.93
<i>Verruca stroemia</i>	0.10	0.04	1.24	99.18
<i>Callopora craticula</i>	0.04	0.02	0.64	99.81
<i>Microporella ciliata</i>	0.00	0.02	0.19	100.00

Regions 2 & 4

Average dissimilarity = 76.21

Species	Shell region 2 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Balanus balanus</i>	3.32	1.30	29.98	29.98
<i>Balanus crenatus</i>	2.32	1.82	23.58	53.56
<i>Conopeum reticulum</i>	0.98	1.06	12.35	65.91
<i>Spirobranchus triqueter</i>	0.26	1.06	10.54	76.45
<i>Celleporella hyalina</i>	0.94	0.48	9.98	86.43
<i>Callopora lineata</i>	0.42	0.10	4.20	90.63
<i>Electra pilosa</i>	0.20	0.18	2.81	93.44
<i>Verruca stroemia</i>	0.08	0.04	1.81	95.25
<i>Cribrilina punctata</i>	0.04	0.14	1.41	96.66
<i>Escharella immersa</i>	0.02	0.10	1.29	97.96
<i>Callopora craticula</i>	0.10	0.02	1.08	99.04
<i>Microporella ciliata</i>	0.06	0.02	0.96	100.00

Regions 3 & 4

Average dissimilarity = 87.26

Species	Shell region 3 Av.Abund	Shell region 4 Av.Abund	Contribution%	Cumulative%
<i>Conopeum reticulum</i>	0.58	1.06	21.83	21.83
<i>Balanus balanus</i>	0.78	1.30	20.26	42.10
<i>Balanus crenatus</i>	0.72	1.82	19.13	61.22
<i>Spirobranchus triqueter</i>	0.30	1.06	18.12	79.34
<i>Celleporella hyalina</i>	0.16	0.48	6.96	86.30
<i>Cribrilina punctata</i>	0.22	0.14	4.53	90.83
<i>Electra pilosa</i>	0.10	0.18	2.83	93.66
<i>Escharella immersa</i>	0.04	0.10	2.59	96.25
<i>Callopora lineata</i>	0.06	0.10	1.63	97.88
<i>Verruca stroemia</i>	0.00	0.04	0.95	98.82
<i>Microporella ciliata</i>	0.02	0.02	0.75	99.58
<i>Callopora craticula</i>	0.02	0.02	0.42	100.00

Appendix E1. Output: SIMPER outcomes showing similarity/dissimilarity of epifaunal community within posterior and anterior shell regions

Posterior region
Average similarity: 26.47

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.55	12.73	0.97	48.10	48.10
<i>Balanus balanus</i>	1.33	3.63	0.49	13.72	61.82
<i>Escharella immersa</i>	0.68	1.66	0.48	6.26	68.08
<i>Spirorbis tridentatus</i>	0.94	1.62	0.42	6.12	74.20
<i>Patinella verrucaria</i>	0.67	1.50	0.42	5.68	79.88
<i>Microporella ciliata</i>	0.61	0.81	0.33	3.05	82.93
<i>Diplosolen obelia</i>	0.47	0.67	0.28	2.53	85.47
<i>Tubulipora phalangea</i>	0.42	0.56	0.27	2.11	87.57
<i>Tubulipora liliacea</i>	0.28	0.32	0.18	1.20	88.77
<i>Electra pilosa</i>	0.33	0.31	0.19	1.19	89.96
<i>Celleporella hyalina</i>	0.31	0.27	0.17	1.01	90.97
<i>Callopora lineata</i>	0.21	0.23	0.15	0.88	91.85
<i>Serpula sp.</i>	0.30	0.23	0.19	0.88	92.73
<i>Schizomavella linearis</i>	0.22	0.21	0.16	0.79	93.51
<i>Scrupocellaria scruposa</i>	0.37	0.20	0.14	0.75	94.26
<i>Balanus crenatus</i>	0.23	0.17	0.10	0.64	94.90
<i>Verruca stroemia</i>	0.17	0.14	0.14	0.53	95.44
<i>Disporella hispida</i>	0.18	0.13	0.12	0.51	95.94
<i>Fenestulina malusii</i>	0.18	0.12	0.13	0.46	96.40
<i>Conopeum reticulum</i>	0.14	0.11	0.08	0.43	96.83
<i>Amphiblestrum flemingii</i>	0.17	0.10	0.13	0.39	97.22
<i>Membraniporella nitida</i>	0.19	0.10	0.10	0.37	97.58
<i>Plagioecia patina</i>	0.14	0.09	0.10	0.34	97.92
<i>Crisia eburnea</i>	0.19	0.09	0.12	0.33	98.25
<i>Chorizopora brongniartii</i>	0.15	0.08	0.10	0.29	98.54
<i>Escharoides coccinea</i>	0.16	0.07	0.08	0.25	98.80
<i>Escharella variolosa</i>	0.13	0.07	0.09	0.25	99.05

<i>Aeta sica</i>	0.16	0.06	0.10	0.24	99.29
<i>Reptadeonella violacea</i>	0.09	0.03	0.06	0.12	99.41
<i>Tubulipora plumosa</i>	0.08	0.03	0.06	0.11	99.52
<i>Tubulipora lobifera</i>	0.09	0.03	0.06	0.10	99.62
<i>Smittoidea reticulata</i>	0.07	0.02	0.05	0.07	99.69
<i>Porella concinna</i>	0.07	0.02	0.06	0.06	99.75
<i>Spirobranchus lamarckii</i>	0.05	0.01	0.04	0.04	99.79
<i>Escharella klugei</i>	0.05	0.01	0.04	0.04	99.82
<i>Stomachetosella sinuosa</i>	0.04	0.01	0.03	0.03	99.85
<i>Crisia aculeata</i>	0.06	0.01	0.04	0.03	99.88
<i>Callopora craticula</i>	0.03	0.00	0.02	0.02	99.90
<i>Hippothoa flagellum</i>	0.03	0.00	0.03	0.02	99.91
<i>Plagioecia sarniensis</i>	0.03	0.00	0.02	0.01	99.93
<i>Parasmittina trispinosa</i>	0.03	0.00	0.02	0.01	99.94
<i>Cribrilina punctata</i>	0.02	0.00	0.02	0.01	99.95
<i>Scruparia chelata</i>	0.03	0.00	0.03	0.01	99.96
<i>Cellepora pumicosa</i>	0.02	0.00	0.02	0.01	99.97
<i>Schizomavella auriculata</i>	0.02	0.00	0.02	0.01	99.98
<i>Scruparia ambiugua</i>	0.03	0.00	0.02	0.01	99.98
<i>Escharella ventricosa</i>	0.02	0.00	0.02	0.01	99.99
<i>Callopora dumerilii</i>	0.02	0.00	0.02	0.01	99.99
<i>Cribrilina annulata</i>	0.02	0.00	0.01	0.00	100.00
<i>Aetea truncata</i>	0.02	0.00	0.01	0.00	100.00
<i>Bugula flabellata</i>	0.01	0.00	0.01	0.00	100.00

Anterior region
Average similarity: 15.07

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	1.42	8.69	0.62	57.64	57.64
<i>Spirorbis tridentatus</i>	0.70	1.58	0.33	10.51	68.15
<i>Escharella immersa</i>	0.44	1.07	0.28	7.10	75.25
<i>Microporella ciliata</i>	0.43	0.66	0.24	4.36	79.61

<i>Patinella verrucaria</i>	0.32	0.58	0.21	3.87	83.48
<i>Balanus balanus</i>	0.27	0.49	0.15	3.27	86.75
<i>Electra pilosa</i>	0.24	0.27	0.13	1.80	88.55
<i>Diplosolen obelia</i>	0.20	0.24	0.14	1.61	90.16
<i>Tubulipora phalangea</i>	0.21	0.24	0.16	1.60	91.76
<i>Conopeum reticulum</i>	0.12	0.16	0.07	1.09	92.85
<i>Fenestrulina malusii</i>	0.16	0.11	0.11	0.75	93.60
<i>Schizomavella linearis</i>	0.13	0.11	0.10	0.71	94.31
<i>Serpula sp.</i>	0.14	0.10	0.08	0.69	95.00
<i>Escharoides coccinea</i>	0.14	0.09	0.09	0.60	95.59
<i>Balanus crenatus</i>	0.12	0.09	0.06	0.59	96.19
<i>Tubulipora liliacea</i>	0.11	0.09	0.08	0.58	96.77
<i>Celleporella hyalina</i>	0.15	0.08	0.08	0.55	97.31
<i>Callopora lineata</i>	0.09	0.06	0.07	0.39	97.70
<i>Membraniporella nitida</i>	0.10	0.05	0.07	0.34	98.04
<i>Reptadeonella violacea</i>	0.06	0.04	0.04	0.27	98.31
<i>Chorizopora brongniartii</i>	0.10	0.04	0.06	0.26	98.57
<i>Disporella hispida</i>	0.06	0.03	0.05	0.23	98.80
<i>Scrupocellaria scruposa</i>	0.09	0.03	0.06	0.22	99.02
<i>Amphiblestrum flemingii</i>	0.07	0.02	0.06	0.16	99.18
<i>Cribrilina punctata</i>	0.04	0.02	0.03	0.11	99.30
<i>Smittoidea reticulata</i>	0.05	0.02	0.04	0.11	99.40
<i>Tubulipora plumosa</i>	0.06	0.01	0.04	0.08	99.48
<i>Verruca stroemia</i>	0.04	0.01	0.03	0.08	99.56
<i>Plagioecia patina</i>	0.05	0.01	0.03	0.08	99.64
<i>Tubulipora lobifera</i>	0.04	0.01	0.03	0.07	99.71
<i>Porella concinna</i>	0.03	0.01	0.02	0.06	99.77
<i>Escharella variolosa</i>	0.03	0.01	0.02	0.05	99.82
<i>Aeta sica</i>	0.04	0.01	0.03	0.05	99.87
<i>Escharella klugei</i>	0.03	0.00	0.02	0.03	99.90
<i>Hippothoa flagellum</i>	0.03	0.00	0.02	0.03	99.92

<i>Cellepora pumicosa</i>	0.02	0.00	0.02	0.02	99.94
<i>Spirobranchus lamarckii</i>	0.02	0.00	0.02	0.02	99.96
<i>Crisia eburnea</i>	0.02	0.00	0.01	0.01	99.97
<i>Stomachetosella sinuosa</i>	0.01	0.00	0.01	0.01	99.98
<i>Scruparia chelata</i>	0.01	0.00	0.01	0.01	99.98
<i>Plagioecia sarniensis</i>	0.01	0.00	0.01	0.00	99.99
<i>Callopora craticula</i>	0.01	0.00	0.01	0.00	99.99
<i>Cribrilina annulata</i>	0.01	0.00	0.01	0.00	99.99
<i>Crisia aculeata</i>	0.01	0.00	0.01	0.00	100.00

Appendix E2. Output: SIMPER outcomes showing similarity/dissimilarity of epifaunal community between posterior and anterior shell regions

Regions posterior & anterior

Average dissimilarity = 81.69

Species	Posterior region Av.Abund	Anterior region Av.Abund	Contribution%	Cumulative%
<i>Spirobranchus triqueter</i>	2.55	1.42	17.63	17.63
<i>Balanus balanus</i>	1.33	0.27	10.05	27.68
<i>Spirorbis tridentatus</i>	0.94	0.70	7.07	34.75
<i>Escharella immersa</i>	0.68	0.44	5.41	40.17
<i>Patinella verrucaria</i>	0.67	0.32	5.14	45.31
<i>Microporella ciliata</i>	0.61	0.43	4.62	49.92
<i>Diplosolen obelia</i>	0.47	0.20	3.49	53.42
<i>Tubulipora phalangea</i>	0.42	0.21	3.24	56.65
<i>Electra pilosa</i>	0.33	0.24	3.02	59.67
<i>Balanus crenatus</i>	0.23	0.12	2.63	62.31
<i>Tubulipora liliacea</i>	0.28	0.11	2.52	64.83
<i>Celleporella hyalina</i>	0.31	0.15	2.51	67.34
<i>Conopeum reticulum</i>	0.14	0.12	2.25	69.59
<i>Scrupocellaria scruposa</i>	0.37	0.09	2.16	71.75
<i>Serpula sp.</i>	0.30	0.14	2.12	73.87

<i>Callopora lineata</i>	0.21	0.09	2.01	75.88
<i>Schizomavella linearis</i>	0.22	0.13	1.91	77.80
<i>Fenestrulina malusii</i>	0.18	0.16	1.73	79.52
<i>Escharoides coccinea</i>	0.16	0.14	1.64	81.16
<i>Membraniporella nitida</i>	0.19	0.10	1.58	82.74
<i>Disporella hispida</i>	0.18	0.06	1.47	84.21
<i>Verruca stroemia</i>	0.17	0.04	1.28	85.49
<i>Chorizopora brongniartii</i>	0.15	0.10	1.28	86.77
<i>Amphiblestrum flemingii</i>	0.17	0.07	1.18	87.95
<i>Plagioecia patina</i>	0.14	0.05	1.16	89.12
<i>Escharella variolosa</i>	0.13	0.03	1.04	90.15
<i>Reptadeonella violacea</i>	0.09	0.06	1.03	91.18
<i>Aeta sica</i>	0.16	0.04	0.99	92.17
<i>Crisia eburnea</i>	0.19	0.02	0.97	93.14
<i>Tubulipora plumosa</i>	0.08	0.06	0.78	93.92
<i>Tubulipora lobifera</i>	0.09	0.04	0.71	94.63
<i>Smittoidea reticulata</i>	0.07	0.05	0.64	95.28
<i>Porella concinna</i>	0.07	0.03	0.50	95.78
<i>Cribrilina punctata</i>	0.02	0.04	0.44	96.22
<i>Escharella klugei</i>	0.05	0.03	0.41	96.63
<i>Spirobranchus lamarckii</i>	0.05	0.02	0.39	97.02
<i>Stomachetosella sinuosa</i>	0.04	0.01	0.33	97.35
<i>Crisia aculeata</i>	0.06	0.01	0.33	97.68
<i>Hippothoa flagellum</i>	0.03	0.03	0.30	97.98
<i>Cellepora pumicosa</i>	0.02	0.02	0.26	98.24
<i>Callopora craticula</i>	0.03	0.01	0.25	98.49
<i>Plagioecia sarniensis</i>	0.03	0.01	0.23	98.72
<i>Parasmittina trispinosa</i>	0.03	0.00	0.21	98.93
<i>Scruparia chelata</i>	0.03	0.01	0.19	99.11
<i>Schizomavella auriculata</i>	0.02	0.00	0.18	99.30
<i>Scruparia ambiugua</i>	0.03	0.00	0.17	99.47

<i>Callopora dumerilii</i>	0.02	0.00	0.11	99.58
<i>Cribrilina annulata</i>	0.02	0.01	0.11	99.69
<i>Escharella ventricosa</i>	0.02	0.00	0.11	99.80
<i>Aetea truncata</i>	0.02	0.00	0.08	99.88
<i>Bugula flabellata</i>	0.01	0.00	0.07	99.94
<i>Bugula turbinata</i>	0.00	0.00	0.04	99.98
<i>Scrupocellaria reptans</i>	0.00	0.00	0.01	99.99
<i>Aetea anguina</i>	0.00	0.00	0.01	100.00

Appendix F. Output: SIMPER outcomes showing similarity/dissimilarity of epifaunal community within each shell size classes

Size class 30-34.9

Average similarity: 53.39

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirorbis tridentatus</i>	2.44	7.17	1.47	13.43	13.43
<i>Membraniporella nitida</i>	1.99	7.03	1.77	13.17	26.60
<i>Spirobranchus triqueter</i>	1.84	6.35	1.87	11.90	38.50
<i>Escharella immersa</i>	1.77	5.89	1.83	11.03	49.52
<i>Diplosolen obelia</i>	1.65	5.77	1.44	10.81	60.33
<i>Schizomavella linearis</i>	1.06	3.09	1.02	5.78	66.11
<i>Escharoides coccinea</i>	1.23	2.88	0.72	5.39	71.50
<i>Amphiblestrum flemingii</i>	0.91	2.58	0.86	4.82	76.33
<i>Patinella verrucaria</i>	1.03	2.43	0.72	4.54	80.87
<i>Tubulipora phalangea</i>	0.77	1.90	0.74	3.57	84.44
<i>Microporella ciliata</i>	0.71	1.65	0.62	3.10	87.53
<i>Smittoidea reticulata</i>	0.66	1.55	0.63	2.90	90.43
<i>Verruca stroemia</i>	0.74	1.51	0.63	2.83	93.26
<i>Tubulipora lobifera</i>	0.61	0.97	0.44	1.83	95.09
<i>Celleporella hyalina</i>	0.66	0.96	0.45	1.80	96.88
<i>Cellepora pumicosa</i>	0.40	0.66	0.37	1.24	98.12
<i>Serpula sp.</i>	0.43	0.36	0.30	0.67	98.79

<i>Plagioecia sarniensis</i>	0.44	0.30	0.22	0.55	99.34
<i>Fenestrulina malusii</i>	0.30	0.22	0.23	0.41	99.75
<i>Plagioecia patina</i>	0.20	0.06	0.09	0.12	99.87
<i>Callopora lineata</i>	0.17	0.04	0.09	0.07	99.94
<i>Tubulipora liliacea</i>	0.13	0.03	0.09	0.06	100.00

Size class 35-39.9

Average similarity: 57.55

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Membraniporella nitida</i>	2.35	9.19	3.69	15.96	15.96
<i>Diplosolen obelia</i>	2.12	8.31	4.30	14.44	30.40
<i>Spirorbis tridentatus</i>	1.94	6.16	1.66	10.70	41.10
<i>Spirobranchus triqueter</i>	1.82	5.53	1.38	9.61	50.71
<i>Microporella ciliata</i>	1.22	4.02	1.65	6.99	57.70
<i>Patinella verrucaria</i>	1.17	3.92	1.63	6.82	64.51
<i>Schizomavella linearis</i>	1.47	3.78	1.10	6.57	71.08
<i>Escharella immersa</i>	1.43	3.77	1.06	6.56	77.64
<i>Escharoides coccinea</i>	1.22	3.26	0.98	5.67	83.31
<i>Tubulipora lobifera</i>	1.14	2.38	0.81	4.14	87.45
<i>Smittoidea reticulata</i>	0.90	1.54	0.58	2.68	90.13
<i>Tubulipora phalangea</i>	0.60	1.33	0.60	2.31	92.45
<i>Amphiblestrum flemingii</i>	0.65	1.33	0.59	2.31	94.76
<i>Tubulipora liliacea</i>	0.68	1.33	0.59	2.31	97.07
<i>Verruca stroemia</i>	0.71	1.23	0.60	2.14	99.21
<i>Disporella hispida</i>	0.27	0.16	0.17	0.28	99.48
<i>Celleporella hyalina</i>	0.43	0.11	0.17	0.19	99.67
<i>Serpula sp.</i>	0.38	0.10	0.17	0.18	99.85
<i>Fenestrulina malusii</i>	0.27	0.09	0.17	0.15	100.00

Size class 40-44.9

Average similarity: 23.88

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	1.56	6.03	1.00	25.24	25.24
<i>Escharella immersa</i>	1.20	3.61	0.78	15.12	40.36
<i>Balanus balanus</i>	1.34	3.14	0.51	13.14	53.50
<i>Patinella verrucaria</i>	0.76	1.61	0.35	6.73	60.23
<i>Schizomavella linearis</i>	0.63	1.35	0.50	5.67	65.90
<i>Escharella variolosa</i>	0.60	0.96	0.34	4.03	69.93

<i>Tubulipora phalangea</i>	0.51	0.80	0.34	3.34	73.26
<i>Chorizopora brongniartii</i>	0.46	0.75	0.32	3.16	76.42
<i>Diplosolen obelia</i>	0.57	0.70	0.31	2.94	79.37
<i>Verruca stroemia</i>	0.33	0.54	0.28	2.25	81.61
<i>Reptadeonella violacea</i>	0.46	0.52	0.21	2.17	83.79
<i>Tubulipora liliacea</i>	0.35	0.48	0.22	2.02	85.80
<i>Microporella ciliata</i>	0.35	0.48	0.33	2.00	87.80
<i>Electra pilosa</i>	0.38	0.47	0.25	1.95	89.75
<i>Spirorbis tridentatus</i>	0.60	0.42	0.22	1.74	91.49
<i>Escharoides coccinea</i>	0.50	0.33	0.19	1.38	92.87
<i>Celleporella hyalina</i>	0.26	0.32	0.11	1.33	94.20
<i>Plagioecia patina</i>	0.30	0.27	0.19	1.14	95.34
<i>Callopora lineata</i>	0.14	0.20	0.09	0.85	96.19
<i>Serpula sp.</i>	0.25	0.18	0.20	0.74	96.93
<i>Fenestulina malusii</i>	0.18	0.15	0.16	0.64	97.57
<i>Membraniporella nitida</i>	0.27	0.14	0.16	0.59	98.16
<i>Smittoidea reticulata</i>	0.23	0.12	0.16	0.50	98.66
<i>Tubulipora lobifera</i>	0.20	0.10	0.13	0.41	99.07
<i>Amphiblestrum flemingii</i>	0.20	0.09	0.13	0.40	99.47
<i>Balanus crenatus</i>	0.14	0.07	0.06	0.30	99.76
<i>Scrupocellaria scruposa</i>	0.14	0.03	0.07	0.12	99.88
<i>Porella concinna</i>	0.09	0.01	0.04	0.06	99.94
<i>Schizomavella auriculata</i>	0.08	0.01	0.04	0.06	100.00

Size class 45-49.9

Average similarity: 33.63

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	2.34	9.91	1.82	29.46	29.46
<i>Patinella verrucaria</i>	1.14	3.50	0.79	10.40	39.86
<i>Escharella immersa</i>	1.30	3.22	0.81	9.59	49.44
<i>Spirorbis tridentatus</i>	1.40	2.53	0.54	7.52	56.96
<i>Balanus balanus</i>	1.44	2.42	0.45	7.19	64.15
<i>Schizomavella linearis</i>	0.88	2.24	0.71	6.66	70.81
<i>Diplosolen obelia</i>	1.08	2.02	0.57	6.01	76.82
<i>Tubulipora liliacea</i>	0.64	1.42	0.41	4.22	81.03
<i>Tubulipora phalangea</i>	0.54	0.75	0.39	2.23	83.27
<i>Escharoides coccinea</i>	0.68	0.66	0.27	1.98	85.24
<i>Escharella variolosa</i>	0.42	0.58	0.26	1.72	86.97

<i>Membraniporella nitida</i>	0.55	0.56	0.29	1.67	88.63
<i>Reptadeonella violacea</i>	0.43	0.55	0.28	1.64	90.27
<i>Microporella ciliata</i>	0.40	0.43	0.32	1.29	91.57
<i>Disporella hispida</i>	0.32	0.42	0.26	1.26	92.82
<i>Serpula</i> sp.	0.38	0.34	0.26	1.00	93.82
<i>Smittoidea reticulata</i>	0.30	0.25	0.24	0.75	94.57
<i>Electra pilosa</i>	0.33	0.25	0.19	0.74	95.31
<i>Fenestrulina malusii</i>	0.27	0.25	0.21	0.73	96.05
<i>Stomachetosella sinuosa</i>	0.26	0.22	0.19	0.66	96.71
<i>Plagioecia patina</i>	0.20	0.20	0.16	0.58	97.29
<i>Chorizopora brongniartii</i>	0.34	0.20	0.17	0.58	97.87
<i>Amphiblestrum flemingii</i>	0.28	0.17	0.20	0.51	98.38
<i>Tubulipora lobifera</i>	0.32	0.17	0.17	0.51	98.90
<i>Verruca stroemia</i>	0.27	0.14	0.17	0.42	99.32
<i>Spirobranchus lamarckii</i>	0.18	0.07	0.10	0.22	99.54
<i>Hippothoa flagellum</i>	0.11	0.05	0.10	0.14	99.67
<i>Schizomavella auriculata</i>	0.11	0.04	0.08	0.12	99.79
<i>Tubulipora plumosa</i>	0.09	0.03	0.08	0.09	99.88
<i>Cellepora pumicosa</i>	0.11	0.02	0.08	0.07	99.95
<i>Escharella ventricosa</i>	0.05	0.01	0.03	0.03	99.98
<i>Aeta sica</i>	0.06	0.01	0.03	0.02	100.00

Size class 50-54.9

Average similarity: 31.12

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	3.61	15.13	1.32	48.60	48.60
<i>Balanus balanus</i>	1.26	3.59	0.52	11.53	60.14
<i>Spirorbis tridentatus</i>	1.50	2.69	0.57	8.65	68.79
<i>Patinella verrucaria</i>	0.89	2.10	0.53	6.75	75.54
<i>Microporella ciliata</i>	1.19	1.91	0.50	6.13	81.68
<i>Escharella immersa</i>	0.72	1.22	0.49	3.91	85.59
<i>Tubulipora phalangea</i>	0.67	1.01	0.38	3.26	88.85
<i>Serpula</i> sp.	0.56	0.65	0.30	2.08	90.93
<i>Electra pilosa</i>	0.59	0.47	0.22	1.51	92.44
<i>Tubulipora liliacea</i>	0.41	0.46	0.25	1.47	93.91
<i>Diplosolen obelia</i>	0.34	0.35	0.22	1.11	95.02
<i>Scrupocellaria scruposa</i>	0.44	0.26	0.19	0.82	95.85
<i>Celleporella hyalina</i>	0.38	0.24	0.17	0.76	96.60
<i>Fenestrulina malusii</i>	0.36	0.18	0.15	0.58	97.18

<i>Callopora lineata</i>	0.23	0.16	0.15	0.51	97.70
<i>Aeta sica</i>	0.28	0.12	0.15	0.39	98.09
<i>Tubulipora plumosa</i>	0.21	0.10	0.13	0.33	98.43
<i>Amphiblestrum flemingii</i>	0.16	0.09	0.14	0.28	98.70
<i>Crisia eburnea</i>	0.19	0.07	0.12	0.23	98.93
<i>Disporella hispida</i>	0.14	0.06	0.10	0.20	99.13
<i>Plagioecia patina</i>	0.12	0.05	0.08	0.17	99.30
<i>Verruca stroemia</i>	0.10	0.05	0.08	0.15	99.45
<i>Balanus crenatus</i>	0.10	0.03	0.05	0.10	99.55
<i>Callopora craticula</i>	0.09	0.03	0.07	0.08	99.63
<i>Escharella klugei</i>	0.08	0.02	0.07	0.08	99.71
<i>Porella concinna</i>	0.09	0.02	0.07	0.06	99.77
<i>Schizomavella linearis</i>	0.08	0.02	0.05	0.05	99.83
<i>Chorizopora brongiartii</i>	0.10	0.01	0.06	0.04	99.87
<i>Scruparia chelata</i>	0.06	0.01	0.04	0.02	99.89
<i>Aetea truncata</i>	0.06	0.01	0.04	0.02	99.91
<i>Spirobranchus lamarckii</i>	0.05	0.01	0.04	0.02	99.93
<i>Callopora dumerilii</i>	0.05	0.01	0.04	0.02	99.96
<i>Hippothoa flagellum</i>	0.06	0.01	0.04	0.02	99.98
<i>Escharella variolosa</i>	0.04	0.00	0.02	0.01	99.98
<i>Crisia aculeata</i>	0.03	0.00	0.02	0.01	99.99
<i>Escharella ventricosa</i>	0.03	0.00	0.02	0.01	100.00

Size class 55-59.9

Average similarity: 29.37

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	3.59	16.83	1.14	57.30	57.30
<i>Balanus balanus</i>	1.20	2.45	0.40	8.33	65.63
<i>Spirorbis tridentatus</i>	1.27	2.05	0.52	6.97	72.60
<i>Patinella verrucaria</i>	0.75	1.29	0.41	4.39	76.99
<i>Microporella ciliata</i>	1.04	1.25	0.40	4.26	81.25
<i>Escharella immersa</i>	0.61	0.90	0.35	3.06	84.31
<i>Tubulipora phalangea</i>	0.53	0.64	0.32	2.16	86.47
<i>Electra pilosa</i>	0.55	0.55	0.26	1.87	88.34
<i>Celleporella hyalina</i>	0.47	0.41	0.25	1.39	89.73
<i>Diplosolen obelia</i>	0.34	0.38	0.25	1.31	91.03
<i>Disporella hispida</i>	0.30	0.33	0.20	1.13	92.16
<i>Scrupocellaria scruposa</i>	0.54	0.31	0.18	1.06	93.22
<i>Fenestrulina malusii</i>	0.32	0.25	0.19	0.86	94.08

<i>Callopora lineata</i>	0.26	0.25	0.18	0.85	94.93
<i>Crisia eburnea</i>	0.36	0.22	0.20	0.75	95.68
<i>Tubulipora liliacea</i>	0.26	0.21	0.16	0.73	96.41
<i>Balanus crenatus</i>	0.24	0.17	0.11	0.59	97.00
<i>Tubulipora plumosa</i>	0.23	0.15	0.16	0.52	97.52
<i>Serpula</i> sp.	0.25	0.13	0.14	0.44	97.96
<i>Plagioecia patina</i>	0.17	0.12	0.11	0.39	98.35
<i>Aeta sica</i>	0.25	0.11	0.14	0.36	98.72
<i>Conopeum reticulum</i>	0.15	0.10	0.07	0.33	99.05
<i>Chorizopora brongniartii</i>	0.21	0.06	0.11	0.20	99.24
<i>Amphiblestrum flemingii</i>	0.15	0.04	0.10	0.15	99.39
<i>Verruca stroemia</i>	0.09	0.03	0.07	0.10	99.50
<i>Cribilina punctata</i>	0.06	0.02	0.05	0.08	99.58
<i>Escharella klugei</i>	0.13	0.02	0.07	0.08	99.66
<i>Porella concinna</i>	0.10	0.02	0.08	0.07	99.73
<i>Schizomavella linearis</i>	0.07	0.01	0.05	0.05	99.78
<i>Parasmittina trispinosa</i>	0.06	0.01	0.04	0.04	99.83
<i>Crisia aculeata</i>	0.11	0.01	0.05	0.04	99.87
<i>Scruparia chelata</i>	0.07	0.01	0.05	0.04	99.91
<i>Scruparia ambiugua</i>	0.06	0.01	0.04	0.03	99.93
<i>Spirobranchus lamarckii</i>	0.07	0.01	0.04	0.02	99.96
<i>Callopora craticula</i>	0.04	0.00	0.03	0.01	99.97
<i>Hippothoa flagellum</i>	0.04	0.00	0.03	0.01	99.98
<i>Plagioecia sarniensis</i>	0.04	0.00	0.03	0.01	99.99
<i>Aetea truncata</i>	0.02	0.00	0.02	0.00	99.99
<i>Escharella variolosa</i>	0.04	0.00	0.02	0.00	100.00

Size class 60-64.9

Average similarity: 33. 48

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	3.13	19.41	1.25	57.97	57.97
<i>Balanus balanus</i>	1.78	5.44	0.72	16.24	74.21
<i>Spirorbis tridentatus</i>	1.17	1.46	0.38	4.35	78.56
<i>Escharella immersa</i>	0.64	0.98	0.39	2.93	81.49
<i>Callopora lineata</i>	0.44	0.97	0.31	2.90	84.40
<i>Conopeum reticulum</i>	0.55	0.89	0.24	2.65	87.05
<i>Balanus crenatus</i>	0.59	0.79	0.24	2.35	89.40
<i>Patinella verrucaria</i>	0.51	0.62	0.28	1.85	91.25
<i>Tubulipora phalangea</i>	0.51	0.47	0.27	1.40	92.65

<i>Microporella ciliata</i>	0.47	0.47	0.27	1.40	94.05
<i>Scrupocellaria scruposa</i>	0.59	0.35	0.16	1.04	95.09
<i>Diplosolen obelia</i>	0.41	0.33	0.22	1.00	96.09
<i>Serpula sp.</i>	0.45	0.32	0.23	0.95	97.04
<i>Celleporella hyalina</i>	0.28	0.25	0.16	0.75	97.79
<i>Disporella hispida</i>	0.25	0.20	0.14	0.61	98.40
<i>Electra pilosa</i>	0.20	0.14	0.13	0.42	98.82
<i>Tubulipora liliacea</i>	0.16	0.08	0.11	0.24	99.06
<i>Plagioecia patina</i>	0.20	0.07	0.12	0.22	99.28
<i>Verruca stroemia</i>	0.11	0.05	0.10	0.16	99.44
<i>Cribrilina punctata</i>	0.11	0.05	0.09	0.15	99.59
<i>Crisia eburnea</i>	0.10	0.02	0.07	0.07	99.65
<i>Amphiblestrum flemingii</i>	0.11	0.02	0.07	0.06	99.71
<i>Porella concinna</i>	0.09	0.02	0.07	0.06	99.77
<i>Parasmittina trispinosa</i>	0.07	0.01	0.04	0.03	99.81
<i>Tubulipora plumosa</i>	0.05	0.01	0.04	0.03	99.84
<i>Escharella klugei</i>	0.09	0.01	0.05	0.03	99.87
<i>Fenestulina malusii</i>	0.05	0.01	0.04	0.03	99.90
<i>Callopora dumerilii</i>	0.06	0.01	0.04	0.02	99.92
<i>Spirobranchus lamarckii</i>	0.05	0.01	0.04	0.02	99.94
<i>Callopora craticula</i>	0.06	0.01	0.04	0.02	99.96
<i>Aeta sica</i>	0.06	0.01	0.04	0.02	99.97
<i>Chorizopora brongniartii</i>	0.06	0.00	0.04	0.01	99.99
<i>Schizomavella linearis</i>	0.05	0.00	0.02	0.01	99.99
<i>Crisia aculeata</i>	0.03	0.00	0.02	0.01	100.00

Size class 65-69.9

Average similarity: 32.81

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Spirobranchus triqueter</i>	3.21	13.32	0.72	40.59	40.59
<i>Balanus balanus</i>	2.42	8.53	0.89	26.00	66.58
<i>Balanus crenatus</i>	1.44	2.76	0.41	8.41	74.99
<i>Conopeum reticulum</i>	0.99	2.74	0.41	8.35	83.34
<i>Escharella immersa</i>	0.77	0.96	0.38	2.92	86.26
<i>Spirorbis tridentatus</i>	1.01	0.61	0.27	1.86	88.12
<i>Scrupocellaria scruposa</i>	0.91	0.56	0.27	1.71	89.83
<i>Callopora lineata</i>	0.48	0.52	0.30	1.57	91.40
<i>Microporella ciliata</i>	0.70	0.44	0.31	1.34	92.74
<i>Cribrilina punctata</i>	0.29	0.42	0.23	1.29	94.04

<i>Serpula</i> sp.	0.52	0.30	0.26	0.93	94.96
<i>Diplosolen obelia</i>	0.50	0.29	0.27	0.89	95.85
<i>Celleporella hyalina</i>	0.26	0.25	0.18	0.77	96.62
<i>Verruca stroemia</i>	0.23	0.22	0.16	0.66	97.28
<i>Patinella verrucaria</i>	0.42	0.20	0.22	0.62	97.90
<i>Disporella hispida</i>	0.29	0.14	0.18	0.42	98.32
<i>Crisia eburnea</i>	0.26	0.11	0.18	0.33	98.65
<i>Electra pilosa</i>	0.12	0.10	0.10	0.29	98.94
<i>Amphiblestrum flemingii</i>	0.25	0.09	0.18	0.29	99.23
<i>Porella concinna</i>	0.22	0.09	0.18	0.28	99.51
<i>Tubulipora phalangea</i>	0.29	0.09	0.14	0.27	99.79
<i>Spirobranchus lamarckii</i>	0.15	0.03	0.10	0.08	99.86
<i>Chorizopora brongniartii</i>	0.14	0.02	0.10	0.07	99.94
<i>Escharella klugei</i>	0.13	0.01	0.06	0.04	99.97
<i>Hippothoa flagellum</i>	0.11	0.01	0.06	0.03	100.00

Appendix G. North-East Atlantic bryozoan competitive interactions, (W): Winning colony, (L): losing colony, (F): fouling

Ramsey Bay, Isle of Man

Shell	Type of interaction	Species
8	Standoff	<i>Electra pilosa</i> x <i>Electra pilosa</i>
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Tubulipora phalangea</i> (W)
	Overgrowth	<i>Fenestrulina malusii</i> (L) x <i>Electra pilosa</i> (W)
	Standoff	<i>Fenestrulina malusii</i> x <i>Electra pilosa</i>
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Callopora craticula</i> (W)
9	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Microporella ciliata</i> (W)
11	Standoff	<i>Microporella ciliata</i> x <i>Microporella ciliata</i>
	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Chorizopora brongniartii</i> (W)
12	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Callopora lineata</i> (W)
	Fouling	<i>Microporella ciliata</i> x <i>Reptadeonella violacea</i> (F)
14	Fouling	<i>Schizomavella linearis</i> x <i>Schizomavella linearis</i> (F)
	Fouling	<i>Schizomavella linearis</i> x <i>Schizomavella linearis</i> (F)
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Patinella verrucaria</i> (W)
15	Standoff	<i>Fenestrulina malusii</i> x <i>Chorizopora brongniartii</i>
	Standoff	<i>Fenestrulina malusii</i> x <i>Chorizopora brongniartii</i>
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Plagioecia sarniensis</i> (W)
16	Overgrowth	<i>Electra pilosa</i> (L) x <i>Chorizopora brongniartii</i> (W)
	Standoff	<i>Microporella ciliata</i> x <i>Chorizopora brongniartii</i>
17	Standoff	<i>Chorizopora brongniartii</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Fenestrulina malusii</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Fenestrulina malusii</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Chorizopora brongniartii</i>
18	Standoff	<i>Chorizopora brongniartii</i> x <i>Microporella ciliata</i>

	Overgrowth	<i>Celleporella hyalina</i> (L) x <i>Electra pilosa</i> (W)
	Fouling	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i> (F)
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Chorizopora brongniartii</i> (W)
19	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Microporella ciliata</i> (W)
20	Standoff	<i>Electra pilosa</i> x <i>Callopora lineata</i>
	Standoff	<i>Fenestrulina malusii</i> x <i>Callopora lineata</i>
21	Standoff	<i>Electra pilosa</i> x <i>Escharella immersa</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Microporella ciliata</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Microporella ciliata</i> (W)
22	Standoff	<i>Chorizopora brongniartii</i> x <i>Callopora lineata</i>
	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Microporella ciliata</i>
	Fouling	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i> (F)
	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Microporella ciliata</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Microporella ciliata</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Microporella ciliata</i> (W)
23	Overgrowth	<i>Electra pilosa</i> (L) x <i>Microporella ciliata</i> (W)
24	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Microporella ciliata</i> (W)
	Standoff	<i>Patinella verrucaria</i> x <i>Microporella ciliata</i>
25	Standoff	<i>Plagioecia patina</i> x <i>Microporella ciliata</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Microporella ciliata</i>
	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
26	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
28	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Callopora lineata</i> (W)
	Fouling	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i> (F)
29	Standoff	<i>Callopora lineata</i> x <i>Microporella ciliata</i>
	Standoff	<i>Callopora lineata</i> x <i>Microporella ciliata</i>
	Standoff	<i>Callopora lineata</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Chorizopora brongniartii</i> x <i>Chorizopora brongniartii</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Microporella ciliata</i>
31	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Patinella verrucaria</i> (W)
32	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Callopora lineata</i> (W)
	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Electra pilosa</i> (W)
	Standoff	<i>Fenestrulina malusii</i> x <i>Fenestrulina malusii</i>
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Fenestrulina malusii</i> (W)
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Fenestrulina malusii</i> (W)
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Patinella verrucaria</i> (W)
33	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
35	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Fenestrulina malusii</i> (W)
	Standoff	<i>Plagioecia patina</i> x <i>Fenestrulina malusii</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Microporella ciliata</i>
36	Standoff	<i>Microporella ciliata</i> x <i>Microporella ciliata</i>
	Standoff	<i>Microporella ciliata</i> x <i>Microporella ciliata</i>
	Standoff	<i>Electra pilosa</i> x <i>Chorizopora brongniartii</i>
37	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Electra pilosa</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Electra pilosa</i> (W)
39	Standoff	<i>Chorizopora brongniartii</i> x <i>Microporella ciliata</i>
	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>

	Standoff	<i>Chorizopora brongniartii</i> x <i>Escharella immersa</i>
40	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
	Standoff	<i>Electra pilosa</i> x <i>Schizomavella linearis</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Escharella immersa</i> (W)
42	Standoff	<i>Chorizopora brongniartii</i> x <i>Fenestulina malusii</i>
	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
	Fouling	<i>Chorizopora brongniartii</i> x <i>Electra pilosa</i> (F)
	Standoff	<i>Chorizopora brongniartii</i> x <i>Microporella ciliata</i>
	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
43	Standoff	<i>Electra pilosa</i> x <i>Escharella immersa</i>
44	Standoff	<i>Electra pilosa</i> x <i>Microporella ciliata</i>
45	Standoff	<i>Fenestulina malusii</i> x <i>Reptadeonella violacea</i>
47	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
48	Standoff	<i>Fenestulina malusii</i> x <i>Escharella immersa</i>
	Fouling	<i>Microporella ciliata</i> x <i>Fenestulina malusii</i> (F)
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Plagioecia sarniensis</i> (W)
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Fenestulina malusii</i> (W)
	Standoff	<i>Fenestulina malusii</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Microporella ciliata</i> x <i>Fenestulina malusii</i>
	Standoff	<i>Microporella ciliata</i> x <i>Fenestulina malusii</i>
	Standoff	<i>Microporella ciliata</i> x <i>Fenestulina malusii</i>
49	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Microporella ciliata</i> (W)
50	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
51	Overgrowth	<i>Electra pilosa</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Microporella ciliata</i> (W)

Karlsruhe wreck, Orkney

Shell	Type of interaction	Species
5	Standoff	<i>Plagioecia patina</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Tubulipora phalangea</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Plagioecia patina</i> (L) x <i>Fenestulina malusii</i> (W)
7	Standoff	<i>Plagioecia patina</i> x <i>Patinella verrucaria</i>
8	Overgrowth	<i>Plagioecia patina</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Reptadeonella violacea</i> (W)
	Standoff	<i>Escharella variolosa</i> x <i>Reptadeonella violacea</i>
	Standoff	<i>Fenestulina malusii</i> x <i>Reptadeonella violacea</i>
	Standoff	<i>Fenestulina malusii</i> x <i>Escharella immersa</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Escharella immersa</i>
9	Standoff	<i>Fenestulina malusii</i> x <i>Escharella variolosa</i>
	Standoff	<i>Escharella variolosa</i> x <i>Escharella variolosa</i>
11	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
	Standoff	<i>Microporella ciliata</i> x <i>Patinella verrucaria</i>
12	Standoff	<i>Fenestulina malusii</i> x <i>Tubulipora liliacea</i>
13	Overgrowth	<i>Plagioecia patina</i> (L) x <i>Plagioecia patina</i> (W)
	Standoff	<i>Plagioecia patina</i> x <i>Microporella ciliata</i>
19	Standoff	<i>Fenestulina malusii</i> x <i>Tubulipora liliacea</i>
20	Standoff	<i>Patinella verrucaria</i> x <i>Escharella immersa</i>
	Standoff	<i>Plagioecia patina</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Tubulipora phalangea</i> x <i>Tubulipora phalangea</i>
22	Standoff	<i>Fenestulina malusii</i> x <i>Microporella ciliata</i>
23	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
	Standoff	<i>Plagioecia patina</i> x <i>Microporella ciliata</i>

31	Standoff	<i>Plagioecia patina</i> x <i>Plagioecia patina</i>
38	Standoff	<i>Patinella verrucaria</i> x <i>Diplosolen obelia</i>
40	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
	Fouling	<i>Parasmittina trispinosa</i> x <i>Escharella immersa</i> (F)
	Fouling	<i>Parasmittina trispinosa</i> x <i>Escharella immersa</i> (F)
	Fouling	<i>Parasmittina trispinosa</i> x <i>Escharella immersa</i> (F)
46	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
50	Standoff	<i>Plagioecia patina</i> x <i>Patinella verrucaria</i>

Skarnsundet West Bridge, Norway

Shell	Type of interaction	Species
2	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Tubulipora phalangea</i>
3	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
7	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
8	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Diplosolen obelia</i> (W)
9	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Patinella verrucaria</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Callopora craticula</i> (W)
10	Fouling	<i>Dispirella hispida</i> x <i>Patinella verrucaria</i> (F)
12	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Tubulipora liliacea</i> (W)
14	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Amphiblestrum flemingii</i> (W)
17	Standoff	<i>Microporella ciliata</i> x <i>Microporella ciliata</i>
	Fouling	<i>Parasmittina trispinosa</i> x <i>Tubulipora phalangea</i> (F)
	Standoff	<i>Plagioecia patina</i> x <i>Plagioecia patina</i>
	Standoff	<i>Parasmittina trispinosa</i> x <i>Tubulipora phalangea</i>
19	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
21	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Diplosolen obelia</i> (W)
22	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella klugei</i> (W)
23	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharella immersa</i> (W)
26	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
33	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
	Standoff	<i>Tubulipora liliacea</i> x <i>Tubulipora liliacea</i>
35	Standoff	<i>Tubulipora liliacea</i> x <i>Tubulipora liliacea</i>
37	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Amphiblestrum flemingii</i> (W)
39	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Diplosolen obelia</i> (W)
40	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
41	Standoff	<i>Escharella immersa</i> x <i>Amphiblestrum flemingii</i>
42	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Tubulipora liliacea</i> x <i>Stomachetosella sinuosa</i>
	Standoff	<i>Tubulipora liliacea</i> x <i>Stomachetosella sinuosa</i>
	Standoff	<i>Tubulipora liliacea</i> x <i>Tubulipora liliacea</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Tubulipora phalangea</i> (W)
	Standoff	<i>Patinella verrucaria</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
44	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Patinella verrucaria</i> (W)
49	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Tubulipora phalangea</i> (W)

North Llŷn Wales

Shell	Type of interaction	Species
1	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
2	Standoff	<i>Reptadeonella violacea</i> x <i>Escharella ventricosa</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Escharella ventricosa</i>
3	Standoff	<i>Reptadeonella violacea</i> x <i>Escharella immersa</i>
	Standoff	<i>Reptadeonella violacea</i> x <i>Reptadeonella violacea</i>
	Overgrowth	<i>Reptadeonella violacea</i> (L) x <i>Reptadeonella violacea</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Chorizopora brongniartii</i> (W)
5	Standoff	<i>Patinella verrucaria</i> x <i>Electra pilosa</i>
6	Standoff	<i>Reptadeonella violacea</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Stomachetosella sinuosa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Stomachetosella sinuosa</i>
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
7	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Diplosolen obelia</i>
10	Overgrowth	<i>Escharella variolosa</i> (L)x <i>Reptadeonella violacea</i> (W)
11	Standoff	<i>Patinella verrucaria</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Schizomavella linearis</i> x <i>Schizomavella linearis</i>
	Standoff	<i>Microporella ciliata</i> x <i>Electra pilosa</i>
12	Fouling	<i>Patinella verrucaria</i> x <i>Escharella immersa</i> (F)
	Standoff	<i>Escharella immersa</i> x <i>Plagioecia patina</i>
13	Overgrowth	<i>Electra pilosa</i> (L) x <i>Reptadeonella violacea</i> (W)
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Reptadeonella violacea</i> (W)
	Standoff	<i>Reptadeonella violacea</i> x <i>Chorizopora brongniartii</i>
	Standoff	<i>Fenestrulina malusii</i> x <i>Chorizopora brongniartii</i>
	Standoff	<i>Fenestrulina malusii</i> x <i>Reptadeonella violacea</i>
	Standoff	<i>Electra pilosa</i> x <i>Reptadeonella violacea</i>
14	Overgrowth	<i>Escharella immersa</i> (L) x <i>Reptadeonella violacea</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Disporella hispida</i> (W)
	Fouling	<i>Reptadeonella violacea</i> x <i>Patinella verrucaria</i> (F)
15	Fouling	<i>Plagioecia patina</i> x <i>Escharella immersa</i> (F)
16	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Stomachetosella sinuosa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Tubulipora liliacea</i>
	Standoff	<i>Escharella immersa</i> x <i>Stomachetosella sinuosa</i>
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Tubulipora liliacea</i> x <i>Schizomavella linearis</i>
17	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Escharella variolosa</i> (W)
18	Overgrowth	<i>Callopora lineata</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Schizomavella linearis</i> x <i>Callopora lineata</i>
19	Standoff	<i>Reptadeonella violacea</i> x <i>Disporella hispida</i>
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Disporella hispida</i> (W)
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Disporella hispida</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Disporella hispida</i> (W)
	Standoff	<i>Electra pilosa</i> x <i>Schizomavella linearis</i>
20	Standoff	<i>Electra pilosa</i> x <i>Plagioecia sarniensis</i>
	Standoff	<i>Electra pilosa</i> x <i>Escharella immersa</i>
21	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharella variolosa</i> (W)
	Standoff	<i>Electra pilosa</i> x <i>Chorizopora brongniartii</i>
	Standoff	<i>Electra pilosa</i> x <i>Escharella variolosa</i>
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Escharella variolosa</i> (W)
	Standoff	<i>Reptadeonella violacea</i> x <i>Escharella variolosa</i>
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>

	Standoff	<i>Escharella immersa</i> x <i>Escharella variolosa</i>
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Escharella variolosa</i> (W)
	Standoff	<i>Schizomavella linearis</i> x <i>Escharella variolosa</i>
22	Standoff	<i>Escharella immersa</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Tubulipora phalangea</i>
23	Fouling	<i>Stomachetosella sinuosa</i> x <i>Reptadeonella violacea</i> (F)
	Overgrowth	<i>Stomachetosella sinuosa</i> (L) x <i>Reptadeonella violacea</i> (W)
	Overgrowth	<i>Tubulipora plumosa</i> (L) x <i>Stomachetosella sinuosa</i> (W)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Reptadeonella violacea</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Reptadeonella violacea</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Schizomavella linearis</i> (W)
24	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Schizomavella linearis</i> (W)
25	Standoff	<i>Reptadeonella violacea</i> x <i>Schizomavella linearis</i>
26	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Schizomavella linearis</i> x <i>Schizomavella linearis</i>
	Standoff	<i>Electra pilosa</i> x <i>Escharella immersa</i>
27	Standoff	<i>Escharella immersa</i> x <i>Stomachetosella sinuosa</i>
	Standoff	<i>Escharella variolosa</i> x <i>Escharella variolosa</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Reptadeonella violacea</i> x <i>Chorizopora brongniartii</i>
28	Overgrowth	<i>Escharella immersa</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Escharella variolosa</i> (L) x <i>Schizomavella linearis</i> (W)
29	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharella variolosa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Diplosolen obelia</i> (W)
31	Standoff	<i>Patinella verrucaria</i> x <i>Stomachetosella sinuosa</i>
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Microporella ciliata</i> (W)
32	Standoff	<i>Escharella immersa</i> x <i>Escharella variolosa</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharella immersa</i> (W)
34	Overgrowth	<i>Stomachetosella sinuosa</i> (L) x <i>Patinella verrucaria</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Schizomavella linearis</i> (W)
35	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharella immersa</i> (W)
36	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Microporella ciliata</i> (W)
	Standoff	<i>Reptadeonella violacea</i> x <i>Chorizopora brongniartii</i>
	Overgrowth	<i>Reptadeonella violacea</i> (L) x <i>Reptadeonella violacea</i> (W)
38	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
42	Standoff	<i>Reptadeonella violacea</i> x <i>Escharella variolosa</i>
44	Standoff	<i>Escharella variolosa</i> x <i>Chorizopora brongniartii</i>
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Patinella verrucaria</i> (W)
	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Disporella hispida</i> (W)
	Standoff	<i>Reptadeonella violacea</i> x <i>Microporella ciliata</i>
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Chorizopora brongniartii</i> (W)
	Overgrowth	<i>Reptadeonella violacea</i> (L) x <i>Electra pilosa</i> (W)
45	Overgrowth	<i>Microporella ciliata</i> (L) <i>Escharella variolosa</i> (W)
46	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Porella concinna</i> (W)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Porella concinna</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Porella concinna</i> (W)
	Fouling	<i>Porella concinna</i> x <i>Chorizopora brongniartii</i> (F)

	Fouling	<i>Diplosolen obelia</i> x <i>Chorizopora brongniartii</i> (F)
47	Overgrowth	<i>Electra pilosa</i> (L) x <i>Tubulipora liliacea</i> (W)
49	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Escharella variolosa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Escharella variolosa</i>
50	Standoff	<i>Electra pilosa</i> x <i>Stomachetosella sinuosa</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Escharella variolosa</i>

Port Appin

Shell	Type of interaction	Species
1	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
6	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Microporella ciliata</i> (W)
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Microporella ciliata</i> x <i>Cribrilina annulata</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Escharella klugei</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella klugei</i> (W)
7	Standoff	<i>Diplosolen obelia</i> x <i>Microporella ciliata</i>
9	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Diplosolen obelia</i> (W)
	Fouling	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i> (F)
10	Fouling	<i>Diplosolen obelia</i> x <i>Escharella immersa</i> (F)
16	Standoff	<i>Escharella immersa</i> x <i>Porella concinna</i>
17	Overgrowth	<i>Chorizopora brongniartii</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Microporella ciliata</i> x <i>Escharella immersa</i>
	Standoff	<i>Microporella ciliata</i> x <i>Diplosolen obelia</i>
20	Overgrowth	<i>Disparella hispida</i> (L) x <i>Porella concinna</i> (W)
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Diplosolen obelia</i> (W)
21	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> x <i>Escharella immersa</i>
22	Standoff	<i>Diplosolen obelia</i> x <i>Disparella hispida</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Tubulipora phalangea</i> (W)
23	Standoff	<i>Chorizopora brongniartii</i> x <i>Microporella ciliata</i>
25	Standoff	<i>Diplosolen obelia</i> x <i>Callopora lineata</i>
27	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Amphiblestrum flemingii</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Patinella verrucaria</i>
28	Standoff	<i>Microporella ciliata</i> x <i>Amphiblestrum flemingii</i>
	Standoff	<i>Microporella ciliata</i> x <i>Amphiblestrum flemingii</i>
29	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Microporella ciliata</i> (W)
	Standoff	<i>Callopora lineata</i> x <i>Cribrilina annulata</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Microporella ciliata</i> (W)
32	Standoff	<i>Diplosolen obelia</i> x <i>Microporella ciliata</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Amphiblestrum flemingii</i> (W)
36	Standoff	<i>Diplosolen obelia</i> x <i>Patinella verrucaria</i>
40	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Disparella hispida</i> (L) x <i>Microporella ciliata</i> (W)
41	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Callopora lineata</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Amphiblestrum flemingii</i> (W)
44	Standoff	<i>Microporella ciliata</i> x <i>Escharella klugei</i>
	Standoff	<i>Microporella ciliata</i> x <i>Patinella verrucaria</i>
47	Standoff	<i>Escharella klugei</i> x <i>Escharella klugei</i>
49	Fouling	<i>Diplosolen obelia</i> x <i>Cribrilina annulata</i>

Noss Head

Shell	Type of interaction	Species
1	Standoff	<i>Escharella immersa</i> x <i>Cribrilina annulata</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Schizomavella linearis</i>
	Fouling	<i>Diplosolen obelia</i> x <i>Cribrilina annulata</i> (F)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Diplosolen obelia</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
	Standoff	<i>Escharoides coccinea</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharoides coccinea</i> (W)
2	Fouling	<i>Membraniporella nitida</i> x <i>Patinella verrucaria</i> (F)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Patinella verrucaria</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Celleporella hyalina</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Diplosolen obelia</i> (W)
3	Standoff	<i>Diplosolen obelia</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Cellepora pumicosa</i> (W)
	Standoff	<i>Patinella verrucaria</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Escharella immersa</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
4	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Patinella verrucaria</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Chorizopora brongniartii</i>
	Standoff	<i>Chorizopora brongniartii</i> x <i>Chorizopora brongniartii</i>
	Fouling	<i>Escharoides coccinea</i> x <i>Amphiblestrum flemingii</i> (F)
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Amphiblestrum flemingii</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharoides coccinea</i> (W)
5	Standoff	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i>
	Standoff	<i>Celleporella hyalina</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Escharella immersa</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Escharella immersa</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Cellepora pumicosa</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Cellepora pumicosa</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Plagioecia sarniensis</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Celleporella hyalina</i> (L) x <i>Plagioecia sarniensis</i> (W)
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Amphiblestrum flemingii</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Amphiblestrum flemingii</i> x <i>Membraniporella nitida</i>
6	Standoff	<i>Schizomavella linearis</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Smittoidea reticulata</i> (W)
7	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Patinella verrucaria</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Patinella verrucaria</i>
8	Standoff	<i>Diplosolen obelia</i> x <i>Amphiblestrum flemingii</i>
	Overgrowth	<i>Amphiblestrum flemingii</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Patinella verrucaria</i>

	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Patinella verrucaria</i>
9	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Patinella verrucaria</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Smittoidea reticulata</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Tubulipora liliacea</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Tubulipora liliacea</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Tubulipora liliacea</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Fenestrulina malusii</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Escharoides coccinea</i> (F)
10	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
	Reciprocal	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Tubulipora phalangea</i> x <i>Smittoidea reticulata</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
11	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Microporella ciliata</i> (W)
12	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Tubulipora phalangea</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Membraniporella nitida</i> (W)
	Standoff	<i>Tubulipora phalangea</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Tubulipora phalangea</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Membraniporella nitida</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Fenestrulina malusii</i> (L) x <i>Tubulipora phalangea</i> (W)
	Overgrowth	<i>Fenestrulina malusii</i> (L) x <i>Membraniporella nitida</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
13	Standoff	<i>Patinella verrucaria</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Tubulipora phalangea</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Amphiblestrum flemingii</i> (L) x <i>Smittoidea reticulata</i> (W)
	Overgrowth	<i>Plagioecia patina</i> (L) x <i>Amphiblestrum flemingii</i> (W)
15	Overgrowth	<i>Fenestrulina malusii</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Tubulipora phalangea</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)
16	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Amphiblestrum flemingii</i> (W)
	Standoff	<i>Amphiblestrum flemingii</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Diplosolen obelia</i>

	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Amphiblestrum flemingii</i> (W)
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Fenestrulina malusii</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Fenestrulina malusii</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Amphiblestrum flemingii</i> (W)
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Membraniporella nitida</i> (W)
	Standoff	<i>Patinella verrucaria</i> x <i>Amphiblestrum flemingii</i>
17	Standoff	<i>Escharoides coccinea</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Escharella immersa</i>
	Fouling	<i>Escharoides coccinea</i> x <i>Membraniporella nitida</i> (F)
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Plagioecia patina</i> (W)
	Standoff	<i>Patinella verrucaria</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Patinella verrucaria</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i>
	Fouling	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i> (F)
18	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Schizomavella linearis</i> x <i>Smittoidea reticulata</i>
	Overgrowth	<i>Smittoidea reticulata</i> (L) x <i>Schizomavella linearis</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Smittoidea reticulata</i> (F)
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Diplosolen obelia</i> (W)
19	Fouling	<i>Diplosolen obelia</i> x <i>Membraniporella nitida</i> (F)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)
	Reciprocal	<i>Diplosolen obelia</i> x <i>Tubulipora phalangea</i>
21	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Celleporella hyalina</i> (W)
	Standoff	<i>Schizomavella linearis</i> x <i>Celleporella hyalina</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Plagioecia patina</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Smittoidea reticulata</i> (W)
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Smittoidea reticulata</i> (W)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Microporella ciliata</i> x <i>Celleporella hyalina</i>
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Membraniporella nitida</i> (W)
22	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Schizomavella linearis</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Smittoidea reticulata</i> (W)
23	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
24	Reciprocal	<i>Diplosolen obelia</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Microporella ciliata</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Membraniporella nitida</i> (W)
	Fouling	<i>Membraniporella nitida</i> x <i>Tubulipora phalangea</i>
25	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Smittoidea reticulata</i>
	Standoff	<i>Schizomavella linearis</i> x <i>Disporella hispida</i>
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Escharella immerse</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
26	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Smittoidea reticulata</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Smittoidea reticulata</i> (F)
	Fouling	<i>Amphiblestrum flemingii</i> x <i>Schizomavella linearis</i> (F)
	Overgrowth	<i>Amphiblestrum flemingii</i> (L) x <i>Schizomavella linearis</i> (W)
	Reciprocal	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Amphiblestrum flemingii</i> (F)
27	Standoff	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Diplosolen obelia</i> (W)

	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Tubulipora phalangea</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Membraniporella nitida</i> x <i>Smittoidea reticulata</i>
	Standoff	<i>Membraniporella nitida</i> x <i>Escharella immersa</i>
28	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
	Standoff	<i>Escharoides coccinea</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Smittoidea reticulata</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
29	Standoff	<i>Escharella immersa</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Amphiblestrum flemingii</i> (W)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Patinella verrucaria</i> (W)
30	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Membraniporella nitida</i>
	Fouling	<i>Escharoides coccinea</i> x <i>Patinella verrucaria</i> (F)
	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
31	Overgrowth	<i>Escharella immersa</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Membraniporella nitida</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Smittoidea reticulata</i> (W)
32	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Tubulipora phalangea</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Smittoidea reticulata</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (W)
33	Overgrowth	<i>Amphiblestrum flemingii</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Smittoidea reticulata</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
34	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Amphiblestrum flemingii</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
35	Standoff	<i>Escharoides coccinea</i> x <i>Smittoidea reticulata</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Smittoidea reticulata</i>
	Fouling	<i>Escharoides coccinea</i> x <i>Cellepora pumicosa</i> (F)
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Escharella immersa</i> (W)
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Membraniporella nitida</i> (W)
36	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Smittoidea reticulata</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i>
37	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)

38	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Fenestrulina malusii</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Schizomavella linearis</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Fenestrulina malusii</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Tubulipora lobifera</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Patinella verrucaria</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Patinella verrucaria</i> (W)
	Fouling	<i>Diplosolen obelia</i> x <i>Patinella verrucaria</i> (F)
	Standoff	<i>Diplosolen obelia</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Patinella verrucaria</i> (W)
	Standoff	<i>Tubulipora lobifera</i> x <i>Patinella verrucaria</i>
	Standoff	<i>Tubulipora lobifera</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
39	Fouling	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i> (F)
	Standoff	<i>Tubulipora lobifera</i> x <i>Amphiblestrum flemingii</i>
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
	Standoff	<i>Escharella immersa</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Escharella immersa</i> x <i>Amphiblestrum flemingii</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharella variolosa</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
40	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Microporella ciliata</i> x <i>Membraniporella nitida</i>
41	Standoff	<i>Tubulipora phalangea</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Patinella verrucaria</i>
42	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Patinella verrucaria</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Diplosolen obelia</i> (W)
43	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Amphiblestrum flemingii</i>
	Standoff	<i>Escharella immersa</i> x <i>Plagioecia patina</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Schizomavella linearis</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Schizomavella linearis</i>
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Escharoides coccinea</i>
	Standoff	<i>Escharella immersa</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Escharoides coccinea</i>
44	Standoff	<i>Escharella immersa</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharella immersa</i> (W)

	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Fouling	<i>Diplosolen obelia</i> x <i>Tubulipora phalangea</i> (F)
45	Standoff	<i>Escharella immersa</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
46	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Schizomavella linearis</i> (W)
	Overgrowth	<i>Tubulipora phalangea</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Diplosolen obelia</i> x <i>Membraniporella nitida</i>
	Standoff	<i>Tubulipora lobifera</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Amphiblestrum flemingii</i> x <i>Smittoidea reticulata</i>
	Overgrowth	<i>Smittoidea reticulata</i> (L) x <i>Escharoides coccinea</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i> (F)
47	Overgrowth	<i>Escharella immersa</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Smittoidea reticulata</i>
	Standoff	<i>Escharoides coccinea</i> x <i>Cellepora pumicosa</i>
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharella immersa</i> (W)
	Standoff	<i>Escharella immersa</i> x <i>Escharella immersa</i>
	Standoff	<i>Cellepora pumicosa</i> x <i>Cellepora pumicosa</i>
48	Overgrowth	<i>Celleporella hyalina</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Tubulipora phalangea</i> x <i>Amphiblestrum flemingii</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Celleporella hyalina</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Membraniporella nitida</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Schizomavella linearis</i> (L) x <i>Amphiblestrum flemingii</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Amphiblestrum flemingii</i> (F)
	Fouling	<i>Escharoides coccinea</i> x <i>Smittoidea reticulata</i> (F)
	Overgrowth	<i>Celleporella hyalina</i> (L) x <i>Escharoides coccinea</i> (W)
	Fouling	<i>Escharoides coccinea</i> x <i>Cellepora pumicosa</i> (F)
49	Standoff	<i>Diplosolen obelia</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Tubulipora lobifera</i> (L) x <i>Diplosolen obelia</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Fouling	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i> (F)
	Fouling	<i>Diplosolen obelia</i> x <i>Escharoides coccinea</i> (F)
	Standoff	<i>Diplosolen obelia</i> x <i>Escharella immersa</i>
	Standoff	<i>Diplosolen obelia</i> x <i>Escharella immersa</i>
	Standoff	<i>Tubulipora lobifera</i> x <i>Diplosolen obelia</i>
	Standoff	<i>Plagioecia patina</i> x <i>Plagioecia patina</i>
	Standoff	<i>Plagioecia patina</i> x <i>Plagioecia patina</i>
	Standoff	<i>Plagioecia patina</i> x <i>Plagioecia patina</i>
	Overgrowth	<i>Smittoidea reticulata</i> (L) x <i>Plagioecia patina</i> (W)
50	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Diplosolen obelia</i> (W)
	Standoff	<i>Tubulipora lobifera</i> x <i>Membraniporella nitida</i>
	Reciprocal	<i>Escharoides coccinea</i> x <i>Diplosolen obelia</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Smittoidea reticulata</i> (W)
	Standoff	<i>Plagioecia patina</i> x <i>Smittoidea reticulata</i>
	Fouling	<i>Plagioecia patina</i> x <i>Escharoides coccinea</i> (F)
	Overgrowth	<i>Patinella verrucaria</i> (L) x <i>Escharoides coccinea</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Membraniporella nitida</i> (W)
	Overgrowth	<i>Diplosolen obelia</i> (L) x <i>Escharoides coccinea</i> (W)
	Standoff	<i>Escharoides coccinea</i> x <i>Escharoides coccinea</i>
	Overgrowth	<i>Escharoides coccinea</i> (L) x <i>Escharoides coccinea</i> (W)

Dornoch Firth

Shell	Type of interaction	Species
1	Standoff	<i>Celleporella hyalina</i> x <i>Callopora lineata</i>
	Overgrowth	<i>Callopora lineata</i> (L) x <i>Electra pilosa</i> (W)
	Standoff	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i>
3	Overgrowth	<i>Conopeum reticulum</i> (L) x <i>Escharella immersa</i> (W)
4	Standoff	<i>Conopeum reticulum</i> x <i>Conopeum reticulum</i>
	Fouling	<i>Conopeum reticulum</i> x <i>Celleporella hyalina</i> (F)
5	Fouling	<i>Electra pilosa</i> x <i>Callopora lineata</i> (F)
	Standoff	<i>Celleporella hyalina</i> x <i>Callopora lineata</i>
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Callopora lineata</i> (W)
6	Standoff	<i>Conopeum reticulum</i> x <i>Callopora lineata</i>
13	Overgrowth	<i>Electra pilosa</i> (L) x <i>Celleporella hyalina</i> (W)
	Standoff	<i>Electra pilosa</i> x <i>Celleporella hyalina</i>
	Standoff	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i>
	Overgrowth	<i>Callopora lineata</i> (L) x <i>Celleporella hyalina</i> (W)
	Overgrowth	<i>Callopora lineata</i> (L) x <i>Callopora lineata</i> (W)
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Callopora lineata</i> (W)
	Standoff	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i>
	Overgrowth	<i>Celleporella hyalina</i> (L) x <i>Celleporella hyalina</i> (W)
	Overgrowth	<i>Callopora lineata</i> (L) x <i>Escharella immersa</i> (W)
20	Standoff	<i>Conopeum reticulum</i> x <i>Conopeum reticulum</i>
24	Standoff	<i>Conopeum reticulum</i> x <i>Cribrilina punctata</i>
	Standoff	<i>Celleporella hyalina</i> x <i>Callopora lineata</i>
26	Overgrowth	<i>Microporella ciliata</i> (L) x <i>Conopeum reticulum</i> (W)
27	Overgrowth	<i>Electra pilosa</i> (L) x <i>Conopeum reticulum</i> (W)
	Standoff	<i>Celleporella hyalina</i> x <i>Callopora lineata</i>
28	Standoff	<i>Conopeum reticulum</i> x <i>Escharella immersa</i>
32	Standoff	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i>
	Standoff	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i>
33	Standoff	<i>Conopeum reticulum</i> x <i>Conopeum reticulum</i>
35	Standoff	<i>Microporella ciliata</i> x <i>Celleporella hyalina</i>
38	Fouling	<i>Escharella immersa</i> x <i>Conopeum reticulum</i> (F)
44	Overgrowth	<i>Escharella immersa</i> (L) x <i>Conopeum reticulum</i> (W)
	Overgrowth	<i>Callopora lineata</i> (L) x <i>Conopeum reticulum</i> (W)
	Overgrowth	<i>Callopora lineata</i> (L) x <i>Conopeum reticulum</i> (W)
47	Standoff	<i>Electra pilosa</i> x <i>Celleporella hyalina</i>
	Overgrowth	<i>Celleporella hyalina</i> (L) x <i>Conopeum reticulum</i> (W)
	Overgrowth	<i>Electra pilosa</i> (L) x <i>Callopora craticula</i> (W)
48	Standoff	<i>Electra pilosa</i> x <i>Celleporella hyalina</i>
	Standoff	<i>Celleporella hyalina</i> x <i>Callopora lineata</i>
	Fouling	<i>Celleporella hyalina</i> x <i>Callopora lineata</i> (F)
	Fouling	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i> (F)
49	Standoff	<i>Celleporella hyalina</i> x <i>Celleporella hyalina</i>

Appendix H. Number of competitive interaction types in all sites and in each individual site

All sites

Competitive interactions	No. of interactions
Standoff	351
Overgrowth	317
Fouling	32
Reciprocal	5

Ramsey Bay, Isle of Man

Competitive interactions	No. of interactions
Standoff	68
Overgrowth	37
Fouling	8

Karlsruhe wreck, Orkney

Competitive interactions	No. of interactions
Standoff	22
Overgrowth	7
Fouling	3

Skarnsundet West Bridge, Norway

Competitive interactions	No. of interactions
Standoff	20
Overgrowth	17
Fouling	2

North Llŷn Wales

Competitive interactions	No. of interactions
Standoff	55
Overgrowth	58
Fouling	6

Port Appin

Competitive interactions	No. of interactions
Standoff	25
Overgrowth	18
Fouling	3

Noss Head

Competitive interactions	No. of interactions
Standoff	140
Overgrowth	164
Fouling	31
Reciprocal	5

Dornoch Firth

Competitive interactions	No. of interactions
Standoff	21
Overgrowth	16
Fouling	5

Appendix I. Qatar habitat records 5th November to 7th November 2015. SACFOR semi-quantitative abundance scale: C = Common, F = Frequent, O = Occasional, R = Rare (Hiscock, 1996)

Chronological dive number	1	2	3&4	5&6	7&8	9&10
Site	1	2	3	5	7	9
Date	11/5/2015	11/5/2015	11/6/2015	11/6/2015	11/7/2015	11/7/2015
Depth (m bsl)	14	16.8	15	22	20	14.2
	Cobbles and small boulders in 14m with some slight current and occasional gorgonians and rare juvenile oysters. Lost fishin net.	Medium rippled sand in 16.8m with some slight current and anthropogenic debris (cable / ropes etc) and comon gorgonians and common juvenile oysters in dense clumps in places, often around gorgonians.	Remnant oyster bed on coral rock with 40% sediment veneer over patches. Live coral patches and rocky material in rough rows along tidal axis.	Poorly sorted sediment in thin veneer of a cm or two over coral rock in 22m. Sporadic lumps of coral rubble and conspicuous whip coral gorgonians with occasional hydroid colonies	Poorly sorted sediment veneer in 20m overlaying large amounts of coral rubble and rock, in places close to the sediment surface, giving rise to dense gorgonian patches and whip corals. Conspicuous cushion stars, fish burrows and upright hydroids. This site had high densities of encrusting bryoans and foliose calcified bryozoan colonies on the gorgonian bases. Large 50 cm-long undulating cross-tide ripples	Patches of coral rubble and knarly coral in 14m of water and a slight current interspersed with patches of poorly-sorted sediment veneers under which were more coral rock and rubble. Common fish burrows and 30% live coral in places. Some large coral colonies reported in the area.
Live coral cover (%)	10	2	15	1	1	30
Finger sponge				R		
Spiky sponge like Dysidea			R		R	O
Tube sponge (grey)					R	
Cup corals	O	O	O	O	O	O
Density of gorgonicea	O	C	C		C	

(no. m-1) 3-15cm						
Whip corals (black and white)				C	C	
Hydroid colonies			F	O	F	O
Hermit crab				R	R	
Oysters (juv.) 1-3cm	R	C	F			O
Oysters adults 3-15cm			C			
Black spine urchins			C			
Pencil urchins			F			R
Non-native brittle star				C		
Cushion stars					F	
Star fish			O		O	
Black squirt			C	R		R
Grey squirt (Looks like Lissoclinum)				R	R	
Didemnid (?)			R		R	
Exposed coral rock			50			
Large rubble boulders 512-1024 mm	1	0				5
Small rubble boulders 256-512 mm	20	0			1	30
Cobbles 64-256 mm	25	0	1	1	2	10
Pebbles 16-64 mm	10	1	2	5	30	5
coral gravel 4-16mm	3	1	2	5	15	5
shell gravel 4-16mm		2	1	5	3	2
Coarse sand 1-4 mm		0	10	25	20	10
Medium sand 0.25-1 mm	25	70	10	25	20	3
Fine sand 0.063-0.25 mm		5	10	30	4	
Mud <0.063 mm		0				
Shells (empty)	6	1	1	1	4	
Artificial	Lost fishing net	Lost rope and drag mark			Lost wire pot	Artificial
For coral frags (1-6):						
Surface relief (even-rugged)	4		4	4	4	5
Texture (smooth-pitted)	4		5	5	5	5
Stability (stable-mobile)	2		2	2	2	2
Scour (none-scoured)	3		4	3	2	2
Silt (none-silted)	1		2	2	2	2
Fissures >10mm (none-many)	3		2	1	2	4
Crevice <10mm (none-many)	1		2	2	2	3
Boulder/cobble/pebble shape (rounded-angular)	2	3	3	3	3	4
Boulder/cobble - on rock						Y
Boulder/cobble - on sediment	Y					Y
Sand on coral / frags	Y					?Y
Tidal streams - estimated kn	0.25	0.25	v slight	v slight	V slight	V slight
Pollution						

For sediment (1-6)						
Surface relief (even-uneven)	2	2	2	2	2	2
Firmness (firm-soft)	2	3	2	2	2	2
Stability (stable-mobile)	3	3	2	2	2	2
Sorting (well-poor)	2	3	4	4	4	4
Mounds / casts	0	0	0	0	0	0
Burrows / holes	C fish burrows	F fish and crusteans	F fish	R Fish	O Fish	C fish burrows
Waves / dunes (>10 cm high)						
Ripples (<10 cm high) cm	3	5		5	10	
Ripple length (cm)	10	15		30	50	

Appendix J. Number of Bryozoan species colonies encrusting on coral rubble across all stations in Qatar

Species	Station 1	Station 2	Station 3	Station 5	Station 7	Station 9	Total
<i>Nolella</i> sp.				1	4		5
<i>Synnotum aegyptiacum</i>	1						1
<i>Aeta ligulata</i>	2					1	3
<i>Biflustra</i> sp.					3		3
<i>Parellisina</i> sp.	2			1		1	4
<i>Akatopora</i> sp.		3		1			4
<i>Smittipora harmeriana</i>	1						1
<i>Odontoporella</i> sp.	2			1			3
<i>Predanophora longiuscula</i>						1	1
<i>Caulibugula</i> sp.	1						1
<i>Puellina egretta</i>	3						3
<i>Poricella robusta</i>	3					26	29
<i>Drepanophora indica</i>	5	1		1			7
<i>Trypostega johnsoulei</i>	25	2	5	4	4	7	47
<i>Chorizopora brongniartii</i>					1		1
<i>Thalamoporella granulata</i>						1	1
<i>Exechonella brasiliensis</i>	4					1	5
<i>Parasmittina raigii</i>	5	7	3				15
<i>Parasmittina egyptiaca</i>	26		25	27	36	14	128
<i>Parasmittina spondylicola</i>	5	1		1	1		8
<i>Schizoporella errata</i>					9		9
<i>Microporella orientalis</i>	1					5	6
<i>Rhynchozoon</i> sp.	8	2		3	20	5	38
<i>Celleporaria</i> sp.1	2				5		7
<i>Celleporaria</i> sp.2			1		1	6	8
Total samples	25	10	25	30	51	27	168
Total species	17	6	4	9	10	11	
Total colonies in site	96	16	34	40	84	68	338

Appendix K. Ramsey Bay, Isle of Man Bryozoa Image J measurements

Chorizopora brongniartii (Audouin, 1826)

Zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Avicularia length (µm)	Avicularia width (µm)	Kenozooids length (µm)	Kenozooids width (µm)
278.99	179.05	41.01	61.72	71.21	75.68	61.72	50.27
298.71	182.51	51.26	87.38	78.24	49.38	100.14	74.64
229.35	238.43	48.19	53.17	84.54	75.79	57.49	46.07
270.86	176.76	55.96	60	94.44	84.07	89.2	58.44
294.7	172.61	48.63	75.96	93.09	55.21	52.72	80.23
272.72	217.61	48.14	81.05	67.42	55.4	56.71	59.78
280.15	220.66	47.26	53.52	82.81	87.14	53.17	34.46
220.17	115.92	55.06	64.23	68.77	69.11	50.64	22.92
241.89	181.47	52.77	60.52	80.27	87.59	56.71	32.82
236.84	150.69	45.9	68.92	92.52	63.24	128.15	38.15
262.32	193.24	48.19	71.4	95.79	62.57	69.72	63.24
266.09	163.8	52.77	73.93	99.21	89.87		
284.28	214.2	43.79	60	118.8	79.58		
190.29	178.58	35.81	45.04	95.73	67.46		
270.34	180.12	43.79	51.26	87.14	48.74		
269.17	206.95	45.85	58.71				
263.91	174.29	42.27	60.17				
266.82	175.73						
249.55	192.05						
253.56	185.8						
269.87	140.74						
308.23	153.6						

Escharella immersa (Fleming, 1828)

Zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Ovicell length (µm)	Ovicell width (µm)
461.37	310.71	62.06	74.64	204.04	205.07
444.38	339.29	70.13	77.84	176.76	246.32
454.96	353.05	64.23	71.65	183.41	232.1
499.38	235.45	73.39	73.5	173.46	227.06
517.12	241.1	60.91	72.85	220.48	186.27
500.95	339.24	70.62	75.68	209.63	158.33
468.13	246.07	76.2	82.53	165.84	243.29
463.23	280.79	66.48	91.7		
470.52	221.79	71.1	91.7		
480.28	206.44	66.64	81.02		
498	218.09	74.07	85.59		
442.09	222.42	67.69	73.82		
451.63	284.86	55.44	86.14		
472.28	256.77	63.86	85.19		
473.75	273.77	67.42	65.68		

Reptadeonella violacea (Johnston, 1847)

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Avicularia length (μm)	Avicularia width (μm)
302.47	188.07	48.19	62.27	44.03	34.08
295.41	186.82	42.64	58.44	29.89	29.8
276.8	178.34	46.42	63.07	38.43	26.13
261.08	173.99	50.9	71.06	43.55	29.8
314.91	190.28	47.03	56.76	37.03	31.84
284.21	211.17	41.32	60.56	50.27	35.66
308.61	188.07	44.03	61.68	53.71	32.42
265.39	211.02	42.08	64.59	42.08	32.82
332.56	196.27	47.26	72.38	49.38	37.8
293.66	180.29	35.59	53.96	56.71	34.08
267.21	223.04	40.81	64.84	44.03	35.81
279.35	168.29	31.84	52.37	48.74	35.81
327.85	161.14	32.82	68.7	46.13	31.84
325	172.97	36.96	66.83	47.7	32.82
264.67	182.74	34.08	58.35	41.26	32.42
268.38	185.45			44.03	38.9
280.42	174.1			49.48	31.93
328.44	194.7			39.57	32.82

Microporella ciliata (Pallas, 1766)

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Avi length (μm)	Avi width (μm)	Ascopore length (μm)	Ascopore width (μm)	Mandible length (μm)	Mandible width (μm)
579.19	529.59	87.59	144.59	128.32	81.92	43.61	55.02	170.2	29.8
603.91	554.81	67.89	154.02	101.28	81.24	39.04	75.65	207.59	36.68
571.06	541.73	87.11	142.15	143.57	82.65	52.92	59.65	142.43	38.43
582.67	482.35	93.99	133.04	148.14	82.65	36.75	62.27	117.63	34.08
527.64	464.07	78.24	130.85	106.94	84.54	28.35	57.35	149.45	34.08
553.03	522.94	82.3	125.5	140.46	83.07	34.91	61.51		
575.71	486.1	68.39	129.07	130.53	77.57	25.32	44.27		
		66.52	123.98	114.46	72.49				
		87.29	132.9	131.95	78.24				
				131.23	72.85				

Fenestrulina malusii (Audouin, 1826)

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Ovicell length (μm)	Ovicell width (μm)	Ascopore length (μm)	Ascopore width (μm)
467.5	389.3	117.12	169.23	295.38	285.72	61.94	114.46
459.04	394	121.13	147.59	248.28	273.89	74.64	102.44
452.35	344.41	71.95	118.43	259.87	295.9	80.23	113.66
431.98	334.45	71.32	134.5	265.87	311.66	76.2	104.2
427.77	402.66	74.39	153.78	293.45	270.67	88.22	115.13
439.33	427.79	98.6	121.5	234.96	302.47	82.18	113.82
358.52	358.52	58.94	145.89	233.63	321.16	67.69	122.45
499.75	463.3	96.39	155.9	197.11	309.15	48.36	73.93
330.96	425.35	88.49	118.34			103.16	126.17

354.5	383.45	96.64	117.48			88.49	102.24
		98.44	92.41			76.86	102.65
						74.95	115.13

Appendix L. Qatar Bryozoa Image J measurements

Synnotum aegyptiacum (Audouin, 1826)

Paired zooid length (µm)	Paired zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Internode length (µm)	Internode width (µm)	Hole length (µm)	Hole width (µm)
258.11	100.27	72.38	49.48	39.17	67.73	69.83	56.62
206.2	110.16	66.12	47.7	41.26	64.23	57.72	53.17
213.12	56.62	120.28	66.52	52.72	105.48	36.68	25.32
158.62	66.95	57.31	38.97	57.31	147.95	23.04	25.32
216.96	78.88	52.72	36.75	43.55	119.23	22.92	20.63
214.2	94.52	187.66	95.43	50.48	133.46	34.46	36.75
144.73	44.51	164.36	46.13			25.21	27.51

Nolella sp.

Zooid length (mm)	Zooid width (mm)	Orifice length (mm)	Stolon width (mm)	Embryos length (mm)	Embryos width (mm)
0.53	0.041	0.035	0.015	0.027	0.017
0.51	0.045	0.032	0.01	0.024	0.026
0.49	0.027	0.031	0.017	0.029	0.02
0.48	0.036	0.021	0.013	0.025	0.019
0.46	0.032	0.031	0.014	0.022	0.024
0.31	0.034	0.024		0.029	0.02
0.47	0.042	0.024		0.029	0.025
0.39	0.034	0.026		0.035	0.015
0.29	0.038	0.027		0.021	0.017
0.56	0.041	0.024		0.024	0.02

Aetea ligulata Busk, 1852

Stem length (µm)	Stem width (µm)	Frontal membrane length (µm)	Frontal membrane width (µm)
853.28	55.78	235.04	83.45
456.79	52.72	126.27	62.27
		241.94	64.23

Biflustra sp.

Zooid length (µm)	Zooid width (µm)	Frontal membrane length (µm)	Frontal membrane width (µm)
179.94	156.49	138.02	117.16
196.15	177.72	147.74	109.77

149.27	161.86	139.56	74.56
166.6	160.88	129.3	73.39
159.11	114.21	144.35	89.02
199.46	161.08	162.13	109.37
215.9	148.59	152.69	97.31
235.67	140.01	123.39	105.48
201.43	146.88	136.18	100.48
245.76	158.91	147.59	87.77
207.72	141.48	179.36	94.07
221.38	149.01	118.34	74.64
246.59	113.89	116.89	82.69
230.21	111.93	120.02	76.34
151.93	113.17	153.25	77.81
205.3	140.31	149.01	82.84
216.96	121.52	126.27	96.72
199.99	127.33	151.46	87.38
199.75	107.77	136.2	95.73
182.09	133.93	142.96	135.33
183.53	130.67	137.57	84.85
207.72	130.69	145.73	111.56
213.21	145.31	139.67	85.59
229.25	126.42	131.97	81.02
215.93	119.23	151.74	95.43
160.55	149.29	147.74	116.89
170	123.98	132.96	97.31
176.58	151.74	137.8	86.29
228.01	171.94	142.59	94.91
201.86	117.12	153.25	87.29

Parellisina sp.

Zooid length (μm)	Zooid width (μm)	Frontal membrane length (μm)	Frontal membrane width (μm)	Ovicell length (μm)	Ovicell width (μm)	Avicularia length (μm)	Avicularia width (μm)
267.59	156.91	214.58	130.21	95.4	75.93	188.88	57.86
326.54	177.49	238.56	250.99	80.5	80.07	182.55	61.68
321.16	201.28	254.21	142.59	76.2	82.69	147.04	56.94
327.28	209.22	260.36	150.06	84.57	110.06	189.11	63.24
321.03	199.55	246.93	155.9	197.96	238.29	170.85	64.72
266.56	184.83	202.64	155.65	101.33	218.4		
302.2	199.55	227.06	142.98	167.16	281.49		
314.63	165.22	233.08	128.32	156.86	211.36		
333.56	199.71	233.83	150.76	238.65	229.64		
281.91	155.9	185.58	133.91	145.37	154.07		
253.63	165.14	203.93	122.34	176.54	253.9		
320.76	154.67	321.18	126.11	201.03	225.6		
292.47	176.76	241.96	146.66	195.2	219.85		
307.41	179.18	213.89	114.62				
297.58	176.04	190.4	140.01				
328.8	178.87	228.62	144.5				
307.23	181.63	247.59	126.42				
275.34	164.12	238.62	151.13				
242.58	191.39	199.91	131.55				
373.74	171.32	245.31	141.78				
396.6	155.16	248.45	122.88				

434.7	187.66	275.8	135.72				
293.23	204.46	258.09	132.82				
419.25	203.11	201.97	157.76				
250.67	149.17	240.98	137.62				
320.83	168.49	314.27	152.41				
417.43	156.7	190.22	125.67				
386.46	195.87	218.76	137.55				
280.45	133.38	290.07	118.17				
311.51	163.92	298	160.23				

Akatopora sp.

Zooid length (µm)	Zooid width (µm)	Frontal membrane length (µm)	Frontal membrane width (µm)	Avicularia length (µm)	Avicularia width (µm)	Kenozooids length (µm)	Kenozooids width (µm)
471.95	333.83	402.05	286.26	471.23	358.56	131.39	25.21
442.76	359.02	373.12	261.11			138.94	64.68
523.44	352.4	292.94	280.48			145.8	102.44
366.29	356.76	390.4	256.86			114.62	55.49
460.36	318.2	368.15	218.27			118.43	60.17
437.65	286.97	347.57	231.72			176.15	71.76
447.57	301.67	347.65	189.54			126.48	81.4
410.51	276.8	361.33	251.75			102.75	63.24
417.52	381.09	340.67	196.21			207.9	115.19
409.08	309.07	331.71	269.58			198	79.58
459.7	240.71	340.94	204.74			145.93	67.42
365.02	314.21	325.58	168.29			136.17	93.09
387.27	325.93	326.48	221.27			200.51	96.72
404.57	311.33	320.04	238.96			152.7	89.52
401.35	267.11	317.29	209.27			234.79	61.68
434.21	298.25	331.56	189.72				

Smittipora harmeriana (Canu & Bassler, 1929)

Zooid length (µm)	Zooid width (µm)	Frontal membrane length (µm)	Frontal membrane width (µm)	Avicularia length (µm)	Avicularia width (µm)
298.42	221	138.02	107.77	298.17	151.37
259.9	188.63	142.52	113.26	340.23	158.1
263.6	208.63	116.08	94.44	442.67	236.14
249.89	233.17	91.27	108.04	447.19	230.68
279.13	252.31	111.77	107.65		
248.11	241.71	117.27	111.95		
316.37	177.64	113.89	126.09		
342.88	204.66	141.24	111.3		
353.52	181.12	132.45	82.84		
301.39	232.93	132.98	81.82		
273.15	204.24	141.04	94.99		
331.68	231.54	135.74	113.47		
227.34	209.26	122.28	123.64		
334.69	199.75	123.98	89.67		
243.1	221.47	108.62	100.48		

285.69	222.76	141.19	107.45		
326.48	224.8	141.61	111.77		
331.68	217.98	128.4	96.53		
334.5	218.59	163.02	123.24		
303.06	257.13	132.29	108.98		
324.27	244.27	118.88	105.68		
220.84	157.25	143.57	100.08		

Odontoporella sp.

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)
273.77	220.19	94.32	90.43
265.32	150.43	116.82	86.99
259.87	190.95	97.93	80.63
272.15	205.17	110.99	84.54
266.76	244.56	108.98	79.74
262.45	221.99	101.75	85.93
264.75	181.57	91.29	79.05
265.87	223.08	99.87	76.2
260.84	196.27	89.29	73.82
290.71	225.38	86.05	78.08
341.71	188.74	97.39	83.95
341.68	197.53	95.79	81.02
286.05	187.84	91.29	71.4
256.21	173.82	91.75	74.25
282.13	167.04	108.13	78.08
283.08	148.18	105.68	87.74
256.86	217.32	106.2	74.25
268.62	117.09	86.99	72.38
237.24	240	84.94	71.98
272.41	174.97	94.52	71.98
371.32	180.86	107.04	66.48
293.81	196.69	104.58	82.18
264.63	176.39	92.72	73.39
344.8	225.01	103.26	83.03
295.72	209.57	91.01	73.39
277.17	162.49	91.35	81.02
267.68	145.71	98.44	80.2
270.72	148.18	78.88	66.64
308.61	161.99	89.43	66.64
266.09	171.94	93.54	78.08

Predanophora longiuscula (Harmer, 1957)

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Ovicell length (μm)	Ovicell width (μm)	Ansestrula length (μm)	Ansestrula width (μm)
180.12	271.04	59.78	64.23	64.92	106.2	205.89	163.27
190.29	142.43	45.39	50.27	81.02	102.24		
198.08	179.71	48.19	67.69	83.1	67.42		
216.09	125.67	40.81	55.44	68.39	89.02		
182.49	136.17	34.91	49.22				
179.81	168.34	46.36	52.92				

160.69	142.74	47.26	57.86				
214.43	157.31	41.83	46.42				
232.67	117.48	53.52	58.76				
196.94	141.78	57.86	48.36				
229.66	176.18	45.21	46.13				
161.22	90.92	56.76	42.27				
161.88	130.03	51.51	51.51				
141.71	80.76	30.84	42.27				
172.97	149.45	31.18	57.31				
165.85	180.12	45.9	52.92				
152.41	114.21	49	57.35				
194.55	170.22	48.63	61.94				
166.28	145.71	66.52	50.48				
183.51	133.46	42.14	55.44				
203.77	131.29	62.27	51.97				
205.07	180.76	55.11	47.2				
193.9	219.52	60.62	49.59				
153.25	222.83	58.44	57.31				
215.54	142.65	54.49	60.3				
211.11	145.37	50.9	44.51				
225.55	171.58						
239.71	135.78						

Caulibugula sp.

Zooid length (µm)	zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Avicularia length (µm)	Avicularia width (µm)	Spine length (µm)
65.11	15.37	57.64	11.95	19.26	6.48	144.24
67.88	22.39	52.92	9.17	20.5	9.67	175.81
73.39	16.81	67.39	12.34	24.69	8.26	104.4
83.31	17.63	54.59	16.53	18.13	7.8	99.69
70.5	19.58	54.41	17.63	22.57	6.56	103.59
77.06	18.33	55.93	16.97	18.84	8	180.93
71.39	20.19	57.64	18.13	19.9	9.28	163.42
74.17	21.03	52.92	15.24	19.8	9.67	134.55
77.57	17.39	66.63	14.49	20.6	8.26	
89.52	17.45	54.88	15.24	25.93	6.87	
69.97	18.84	58.06	16.01	22.92	6.48	
72.7	17.39	51.51	15.13	20.53	9.45	
62.25	19.72	56.56	13.79	21.74	7.24	
68.39	16.01	49.98	14.67	19.72	7.46	
67.7	19.72	51.71	15.37	20.35	6.87	
66.02	16.68	53.51	12.38	23.24	7.24	
67.42	19.15	54.41	12.51	23.99	7.8	
65.97	18.13	52.55	15.13	19.58	8.2	
87.86	18.9	52.27	12.96	22.13	9.45	
65.89	16.97	64.16	12.68	18.9	7.24	
71.65	16.81	52.32	16.04	23.91	8	
72.44	20.75	56	13.32	22.57	8	
66.63	18.25	54.37	16.81	22.5	6.56	
69.81	20.42	53.71	11.95	23.19	8.26	
75.51	19.07	52.92	13.04	23.13	7.17	
65.23	22.17	48.61	15.64	20.19	7.39	
67.6	16.53	50.76	7.39	21.13	8.81	
60.52	23.6	52.55	16.04	22.13	7.24	

69.83	18.25	53.32	12.51	21.94	8	
65.58	20.75	49.29	14.27			

Puellina egretta Ryland & Hayward, 1992

Zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Ovicell length (µm)	Ovicell width (µm)	Avicularia length (µm)	Avicularia width (µm)
341.55	168.35	40.54	63.1	124	116.72	214.35	136.45
248.96	169.22	44.98	63.04	116.34	152.53	207.26	127.06
303.73	215.27	43.66	63.27	132.43	142.25	193.43	204.16
199.41	154.43	30.82	62.86	130.18	110.05	194.67	135.38
273.55	165.66	43.58	60.74	115.55	131.1	246.08	144.87
276.81	194.24	32.54	70.94	106.61	115.24		
185.15	145.44	43.58	60.74	117.34	133.5		
233.65	179.22	36.76	76.11	116.25	109.52		
272.13	176.19	34.61	62.22	100.55	113.64		
245.1	253.1	40.9	58.47	119.71	152.98		
292.5	262.89	31.52	60.74	108.11	142.25		
184.93	202.14	53.24	65.31	124.24	122.58		
341.84	172.47	35.24	44	110.25	110.02		
323.54	208.58	36.36	47.2	124.59	140.18		
265.87	222.61	41.96	56.24	119.04	132.54		
302.38	148.87	48.95	63.1	130.18	120.41		
319.43	189.98	29.23	58.22	93.66	114.73		
177.82	165.75	28.73	66.75	104.43	140.96		
257.95	194.84	41.34	48.72	154.81	119.41		
227.24	176.92	26.62	48.72				
221.84	166.52	35.24	55.72				
259.15	195.14	34.4	46.03				
259.53	247.78	43.24	50.99				
255.96	182.53	25.5	52.48				
266.84	175.68	26.62	85.89				
187.03	224.32	58.22	42.73				
265.97	236.75	43.24	73.02				
205.83	205.42	38.7	70.32				
294.64	228.63	38.22	51.35				
267.44	235.4	42.73	57.84				

Poricella robusta (Hincks, 1884)

Zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Ovicell length (µm)	Ovicell width (µm)	Avicularia length (µm)	Avicularia width (µm)
233.69	169.78	79.58	62.95	134.55	160.15	150.85	32.82
197.21	153.25	68.16	61.94	149.71	176.76	177.6	36.75
219.41	110.63	97.31	68.77	137.85	228.63	183.91	26.13
206.53	83.32	84.85	61.94	133.145	215.46	177.94	27.98
191.65	108.72	85.1	55.21	151.6	259.66	176.7	35.59
244.79	119.41	74.64	62.27	110.28	228.39	156.24	30.75
239.75	167.6	89.02	52.77	159.04	219.174	151.32	34.46
226.35	147.04	89.67	64.23	119.3	246.11	195.84	45.15
243.1	118.96	87.74	71.21	89.87	232.01	138.48	41.01
213.25	133.51	87.74	67.73			144.5	47.7

209.87	175.8	80.5	70.32			137.93	40.03
209.11	183.53	87.86	68.81			160.49	34.46
246.16	95.35	96.01	62.36			170.63	41.83
210.92	114.46	87.14	61.04			177.41	32.58
205.89	155.96	69.98	56.38			181.82	30.75
238.3	156.31	78.08	58.44			136.2	31.18
236.53	100.71	101.52	71.1			176.92	37.94
236.34	162.91	101.8	79.15			164.07	39.04
201.86	126.27	101.52	59.6			158.06	34.08
252.23	135.33	98.81	65.24			193.67	41.32
242.37	171.81	89.43	64.23			197.49	47.26
233.85	118.96	96.31	66.52			145.8	39.17
230.77	149.87	94.02	69.72			213.64	49.06
229.43	146.02	100.08	65.64			180.77	51.26
256.37	130.85	94.02	61.89			141.19	38.15
234.73	96.53	80.53	61.94			202.27	50.43
226.63	85.59	91.73	81.92			201.91	50.48
215.84	130.67	99.19	69.72			228.81	46.07
224.54	153.87	95.4	61.89			210.53	36.75
249.55	153.6	105.68	68.96			196.69	44.03

Drepanophora indica Hayward, 1988

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Ovicell length (μm)	Ovicell width (μm)
129.07	110.16	54.33	72.99	214.45	357.51
165.47	84	48.37	71.02	207.16	290.17
137.19	88.2	62	78.1	191.76	270.88
192	96.75	62.13	74.43	136.31	244.66
178.1	94.15	56.32	65.97	203.9	331.49
168.96	87.36	57.58	65.79	147.65	286
135.07	92.78	64.62	60.03	174.47	314.13
127.31	106.92	52.8	58.82	88.57	276.35
165.47	88.54	42.52	65.51	161.91	244.01
130	97.1	58.41	69.97		
141.72	85.44	92.2	55.71		
148.49	94.76	65.12	53.81		
156.82	92.09	58.41	67.88		
138.81	108.98	52.35	70.94		
154.31	106.08	43.86	63.78		
142.06	110	45.65	60.73		
114	105.39	58.82	60.93		
130.38	111.09	39.6	73.54		
156.82	90.02	59.36	49.48		
154.98	104.31	42.43	67.05		
114.77	88.02	58.14	61.19		
154.32	94.02	72.25	73.76		
160.46	74.03	72.44	58.41		
160.82	84.21	64.78	67.68		
155.67	68.12	51.61	66.48		
142.23	92.02	76.58	66.48		
166.05	97.02	64.4	67.2		
160.56	78.92	68.82	75.15		
143.74	98.18	55.03	64.9		
151.38	101.98	68.26	79.25		

Trypostega johnsoulei Tilbrook, 2006

Zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Ovicell length (µm)	Ovicell width (µm)	Kenozooids length (µm)	Kenozooids width (µm)
359.54	205.25	59.67	57.2	332.3	306.16	75.29	56.36
337.2	214.4	53.74	53.74	234.08	240.01	54.04	72.8
394.69	196.58	58.14	53.25	242.99	256.78	60.93	53.67
316.51	233.53	63.25	52.5	262.49	259.75	72.11	56.57
413.57	177.05	64.03	53.67	258.07	258.94	62.13	67.94
380.87	164.15	62.8	55.32			80.22	62.29
290.03	197.63	61.77	54.92			79.85	67.68
326.34	223.52	48.37	45.65			55.46	53.85
394.59	260.54	67.08	53.67			65.3	74.97
326.1	222	60.96	52.8			55.03	65.3
392.86	167.52	58.14	58.31			58.14	62.23
379.39	149.25	59.4	56.57			50.99	54.92
382.96	225.29	57.2	53.85			87.93	61.74
301.68	222.4	62.61	52			64.78	50.64
393.8	201.79	54.59	48.83			92.2	58.82
359.45	204.98	55.32	49.68			87.2	50.36
397.96	208.1	62.48	49.68			64.9	60.13
367.48	231.48	64.03	49.52			90.91	62.77
345.4	194.59	60.83	55.17			63.66	52.5
373.15	214	58.55	51.22			80.45	62.64
345.32	186.29	51.42	52			73.35	60
341.2	205.91	56.04	53.85			56.36	69.86
340.85	203.58	62.77	55.17			66.48	67.05
376.09	215.42	59.93	54.59			111.57	69.57
341.98	198.28	50.48	48.66			74	77.67
358.09	170.29	51.92	55.03			54.92	72.25
404	232.77	58	60.13			64	68.26
390.13	236.41	60	54.92			66.75	68.47
342.29	222.14	56	60			68.26	70
365.4	242.21	56.04	54			102.49	65.15

Chorizopora brongniartii (Audouin, 1826)

zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Ovicell length (µm)	Ovicell width (µm)	Avi length (µm)	Avi width (µm)	Kenozooids length (µm)	Kenozooids width (µm)
163.04	94.41	37.6	42.14	74.95	90.46	66.16	52.72	69.72	33.06
162.1	112.8	37.03	46.36	76.86	87.38	55.02	57.72	29.8	39.57
138.5	124.77	32.42	52.92	83.03	85.65	63.57	36.96	59.6	41.52
181.38	118.01	39.57	45.04	79.58	79.58	33.84	43.25	64.55	45.04
183.91	123.98	40.55	35.88	81.92	80.76	34.38	46.42	51.97	68.04
202.57	114.71	31.18	48.57	85.84	93.99	32.82	49	63.86	21.74
218.22	119.56	30.84	44.09	77.57	87.74	39.57	39.04	60	48.57
212.7	112.91	32.82	34.08	78.08	80.23	46.13	36.96	54.34	52.92
192.58	126.09	29.17	29.89	86.29	76.31	57.35	59.65	46.13	30.75
186.93	103.44	33.38	49.48	84.85	93.09	57.31	39.17	79.97	52.32
201.74	124.32	31.18	29.8	92.84	89.52	53.66	52.77	55.82	55.82
207.14	106.67	33.38	32.42	84.82	93.65	40.03	34.08	45.9	46.07
227.42	92.07	38.43	39.04	75.96	89.9	64.19	61.89	55.82	37.8
217.55	114.46	35.88	34.91	68.77	74.85	53.17	45.9	64.55	48.57
179.75	99.53	36.24	35.59	77.06	96.72	40.1	44.51	68.16	76.89

103.29	119.23	36.24	48.63	69.87	79.44	45.85	49.59	68.39	61.51
175.63	96.74	35.06	44.09	65.68	79.84	45.67	56.94	43.79	35.06
193.24	119.67	31.18	49	69.38	96.42	62.61	45.5	51.51	34.91
232.03	114.02	30.15	46.07	98.68	86.29	45.04	55.06	108.62	91.35
192.92	135.12	41.01	45.04			48.36	57.49	56.2	43.49
172.24	112.77	32.42	61.17			32.58	42.27	61.89	61.94
128.87	147	38.43	60.17			50.27	47.2		
167.37	123.13	30.75	57.45			52.27	55.44		
207.14	100.89	34.91	52.37						
182.03	105.68	45.85	49.06						
158.99	119.56	30.75	57.86						
193.79	114.9	38.97	50.9						
214.28	105.18	34.08	40.55						
217.97	87.14	38.15	55.44						
104.55	81.24	46.42	52.77						

Thalamoporella granulata Levinsen, 1909

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Avicularia length (μm)	Avicularia width (μm)	Mandible length (μm)	Mandible width (μm)
326.31	144.35	89.2	74.67	383.1	144.93	217.51	104.6
372.58	153.05	96.39	100.89				
283.02	152.15	92.21	89.2				
295.8	135.95	83.45	71.98				
312.9	126.27	94.07	81.31				
359.75	118.34	103.87	91.7				
303.76	145.59	95.65	87.77				
338.95	141.48	90.69	82.84				
313.96	177.72	91.52	85.59				
273.34	170.89	51.26	73.39				
331.97	223.17	68.7	50.27				
298.98	133.28	55.44	80.76				
304.07	198	89.67	89.52				
278.84	149.03	82.81	82.56				
314.21	158.71	85.1	85.59				
255.29	157.45	71.4	90.14				
281.16	166.2	84.82	79.74				
256.78	141.41	82.65	92.41				
319.84	100.55	89.9	86.29				
302.07	125.08	98.6	85.28				
214.63	129.78	108.91	89.02				
256.77	128.32	100.48	94.32				
298.27	233.08	80.07	83.45				
220.17	291.18	102.24	84.07				
272.46	145.31	81.4	73.93				
251.39	155.65	87.14	87.14				
350.66	129.11	89.02	74.39				
252.17	129.76	97.93	77.94				
263.88	149.71	91.27	84.1				
261.89	166.14	91.29	86.42				

Exechonella brasiliensis Canu & Bassler, 1928

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Peristome length (μm)
256.64	201.66	60.17	75.93	30.84
267.82	192.71	64.19	66.52	27.98
266.85	190.22	69.38	71.4	34.38
234.96	163.15	63.86	71.17	44.09
220.68	181.57	53.32	69.72	36.24
293.52	201.87	69.38	73.68	31.18
301.53	188.49	64.23	59.6	28.72
291.69	206.53	57.86	69.98	38.44
225.08	190.95	55.44	75.09	31.84
238.52	172.93	54.49	66	44.09
262.77	149.7	59.47	67.73	34.08
297.01	261.34	62.61	48.36	25.63
297.19	182.55	44.51	74.39	23.6
256.51	191.39	48.57	57.31	39.17
274.08	209.53	64.84	66.16	41.26
224.85	185.12	52.72	59.6	34.08
270.76	187.09	54.49	80.5	32.82
255.71	156.91	66.12	72.38	31.18
232.46	155.43	63.86	62.57	42.64
276.86	150.06	67.42	54.34	
215.54	106.86	43.07	68.39	
263.33	185.68	52.92	65.24	
241.58	138.56	52.77	73.39	
123.45	88.196	44.09	48.14	
185.82	124.72	55.06	59.65	
233.53	145.71	63.94	81.4	
256.37	177.49	49.38	66.16	
252.81	158.78	69.11	74.25	
199.34	134.5	62.95	64.19	
270.76	270.52	71.62	61.68	

Parasmittina raigii (Audouin, 1826)

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Ovicell length (μm)	Ovicell width (μm)	Avi length B (μm)	Avi width B (μm)	Avi length S (μm)	Avi width S (μm)
233.94	186.59	72.82	66.83	120.65	148.75	257.17	94.1	69.83	38.43
272.99	177.47	62.57	71.21	117.48	174.14	218.99	55.78	95.76	49.48
215.84	160.47	55.44	69.38	104.98	143.53	178.31	49	69.61	35.59
271.11	200.81	63.07	65.64	91.61	169.86	172.93	40.03	60.69	38.97
289.3	230.83	65.2	75.09	101.49	143.62	153.34	70.8	79.05	26.83
277.24	183.7	68.7	69.72	92.84	140.65	128.46	56.62	81.31	28.35
229.09	191.76	60.52	71.21	90.69	161.79	117.72	64.35	58.44	31.18
372.16	142.21	56.62	69.98	105.68	150.71	122.56	64.55	74.64	36.24
187.83	151.86	61.72	65.64	120.13	153.61			68.81	34.91
267.12	166.07	53.32	55.11	106.2	171.09			55.21	26.13
270.72	200.29	58.44	71.65	98.6	139.46			72.82	39.44
294.39	250.67	55.82	65.64	101.1	155.89			49.59	29.17
313.75	193.36	59.51	70.13	108.93	160.49			76.2	39.17
395.55	204.35	55.4	66.12	110.06	165.84			66.76	37.32
267.12	201.75	57.31	61.94	100.55	152.41			81.4	37.8

231.49	156.04	62.06	71.65	97.31	160.05			75.09	39.17
303.07	205.11	64.84	62.06	97.74	167.16			80.07	41.83
291.8	224.68	73.93	66.52	104.98	166.47			66.64	41.01
242.98	163.02	71.1	75.79	94.24	167.92				
348.62	158.99	57.72	66.83	103.19	147.59				
279.24	198.5	61.89	71.4	108.72	141.48				
350.39	163.8	66.83	66.52	115.19	155.9				
303.17	222.67	51.51	67.11	112.42	176.58				
324.06	183.63	59.65	66.48	125.42	146.31				
276.06	202.79	55.11	55.11	124.26	162.38				
318.6	220.19	57.49	73.39	117.12	134.92				
273.77	227.89	61.94	64.23	110.73	151.93				
344.97	177.72	66.52	71.21	152.51	116.71				
286.56	177.06	67.11	71.4	111.41	160.05				
350.3	184.56	60.91	54.49	76.34	107.43				

Avi= avicularia, S=small, B=Big

Parasmittina egyptiaca (Waters, 1909)

Zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Ovicell length (µm)	Ovicell width (µm)	Avicularia length B (µm)
325.49	125.68	42.84	43.75	151.79	194.31	150.06
236.14	112.69	44.08	41.07	240.98	288.76	152.22
246.16	121.32	32.81	43.75	227.42	303.8	138.23
284.32	125.34	45.13	41.14	262.16	302.28	108.64
195.8	117.52	45.96	49.65	211.07	271.48	137.36
192.06	108.64	41.7	42.29	121.07	142.98	123.42
190.94	140.64	44.54	34.84			99.05
164.68	104.71	49.65	34.54			68.07
178.18	113.58	43.65	32.99			96.04
215.76	109.34	40.31	37.31			125.65
203.74	137.21	36.67	33.9			149.17
154.55	139.81	43.01	40.2			157.24
175.15	133.66	39.43	37.31			174.95
177.69	158.91	35.91	35.91			145.95
191.83	135.3	45.96	46.15			157.77
172.33	120.74	55.01	48.37			
186.55	120.79	47.12	47.49			
170.22	111.36	51.39	44.35			
144.14	130.51	50.96	42.26			
147.82	116.19	53.61	41.88			
120.74	106.2	53.47	43.11			
159.61	88.25	59.66	46.4			
192.56	128.12	59.3	42.29			
174.38	106.58	63.78	38.19			
169.11	98.58	50.79	46.62			
170.7	114.2	39.88	39.88			
136.77	114.85	39.73	39.88			
160.34	96.9	39.88	38.54			
152.89	106.98	36.87	38.95			
160.61	121.62	46.9	36.52			

Avicularia width B (µm)	Avicularia length S (µm)	Avicularia width S (µm)	Ansestrula length (µm)	Ansestrula width (µm)	Mandible length (µm)	Mandible width (µm)
35.67	32.63	19.92	37.89	24.03	109.17	22.91
34.16	45.99	21.13	113.24	50	113.58	30.79
30.79	44.71	19.1			109.38	15.75
28.63	41.07	11.46			84.28	15.37
35.91	34.03	15.75			114.2	21.87
24.28	43.55	20.57			68.03	28.99
42.19	43.21	20.64			46.25	11.95
14.08	35.21	16.11			78.52	12.31
24.28	37.31	20.64			94.22	9.66
32.81	32.09	21.6			138.74	27.8
42.19	37.93	20.64			139.64	31.91
41.88	24.63	19.47			148.16	24.15
42.01	37.5	25.39			123.68	21.4
32.41	29.83	13.01			131.27	23.23
38.73	40.6	20.78			99.14	22.27
	34.33	22.2				
	57.29	21.6				
	35.67	15.37				
	36.67	20.57				
	34.37	27.59				
	53.47	15.28				
	32.86	19.47				
	55.19	20.57				
	42.7	22.46				
	34.59	24.63				
	44.84	26.52				
	42.19	16.11				
	39.99	22.91				
	41.7	19.99				
	35.91	22.79				

Parasmittina spondylica Harmelin, Bitar & Zibrowius, 2009

Zooid length (µm)	Zooid width (µm)	Orifice length (µm)	Orifice width (µm)	Ovicell length (µm)	Ovicell width (µm)	Avicularia length (µm)	Avicularia width (µm)
288.89	103.79	47.26	47.7	79.84	61	91.7	21.13
242.28	153.87	42.27	53.71	86.29	103.79	97.15	24.69
243.16	139.56	60	56.94	75.2	115.19	94.07	16.53
234.24	146.79	64.92	50.27	87.59	108.62	103.67	16.04
244.79	131.13	48.36	71.4	88.49	108.62	86.99	30.15
211.95	157.31	56.62	60.52	87.77	100.97	104.55	29.17
297.01	109.58	45.39	63.57	85.28	120.98	84.57	27.7
253.98	123.58	60.52	74.85	89.02	107.45	86.42	30.75
239.94	149.45	55.49	50.9	101.75	111.56	90.69	32.82
236.66	173.52	61.94	57.86	93.65	114.83	90.43	34.08
295.19	133.08	60.3	53.71	98.68	116.46	89.4	23.37
255.99	137.87	66.95	69.72	67.73	122.04	102.24	20.5
258.32	121.5	51.97	63.69	84.85	102.34	68.04	34.38
256.28	218.22	73.14	69.72	87.38	116.46	94.41	29.89
256.86	184.83	71.1	74.64	112.54	113.24	66.8	22.69
238.42	171.46	64.35	74.39	79.58	114.99	87.29	30.84
238.3	186.82	74.64	68.16	82.84	126.33	94.99	31.18

228.05	135.78	65.24	64.23	88.55	133.53		
254.48	144.35	52.77	72.85	82.84	108.69		
242.84	169.04	65.68	73.82				
234.29	187.98	50.48	68.81				
222.76	150.69	66.48	77.94				
236.69	156.86	73.5	61.89				
266.29	212.51	79.48	69.72				
215.6	184.9	69.38	87.38				
311.01	204.28	81.4	67.46				
303.58	175.75	102.34	63.57				
252.43	207.3	60.69	88.58				

Schizoporella errata (Waters, 1878)

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Ovicell length (μm)	Ovicell width (μm)	Avicularia length (μm)	Avicularia width (μm)
312.08	202.01	98.68	94.1	159.64	182.02	74.85	34.08
293.31	295.13	87.59	101.1	130.69	220.48	77.98	33.06
334.19	200.86	90.14	98.6	196.21	239.22	78.08	42.14
334.4	249.98	76.31	87.74	141.19	177.59	60.52	42.27
331.85	167.23	82.69	89.29	186.19	164.76	66	42.14
263.89	345.63	81.31	90.34	257.52	168.29	71.8	39.24
325.95	206.81	98.44	95.54	236.69	136.32	76.89	42.14
332.69	156.04	93.57	87.74	215.54	180.92		
242.28	229.9	82.53	100.97	202.95	144.73		
319.31	207.4	88.55	97.53	197.65	162.13		
289.55	237.06	95.35	94.32	194.01	150.76		
338.33	356.49	87.14	89.52	192.69	160.55		
301.37	260.06	80.23	96.39	191.21	142.21		
247.97	265.93	82.81	100.3				
275.86	312.62	93.99	87.38				
266.5	293.63	79.74	93.54				
299.43	248.79	84.07	93.57				
264.63	305.73	72.82	85.31				
297.72	253.56	84.82	87.14				
315.18	257.43	85.1	89.52				
268.31	266.02	80.63	89.17				
279.24	289.74	71.76	91.29				
278.44	254.47	85.59	89.52				
320.2	220.48	72.38	80.63				
257.7	262.24	74.39	89.02				

Microporella orientalis Harmer, 1957

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Ovicell length (μm)	Ovicell width (μm)
369.6	304.91	50.27	82.69	140.76	187.14
332.48	295.06	53.47	84.07	119.3	193.06
370.8	282.97	53.32	74.39	159.52	188.07
383.04	302.31	47.26	73.25	142.59	189.67
341.96	271.88	50.43	81.05	141.19	195.87
317.68	235.32	43.49	61.51	115.38	199.45
368.64	315.62	50.43	69.61	117.52	233.08

321.11	284.31	52.77	75.79		
304.57	265.39	34.69	64.84		
290.93	233.17	44.03	73.14		
328.14	229.54	63.07	60.91		
267.12	279.84	33.38	72.49		
351.66	323.31	64.55	44.51		
332.48	314.28	43.55	61.17		
342.64	242.55	55.44	63.4		
346.24	257.43	53.66	74		
370.49	253.43	42.27	54.49		
354.74	278	52.92	67.11		
358.28	310.23	58.44	83.67		
310.57	250.81	48.74	66.12		
340.81	269.27	52.27	78.08		

Avicularia length (μm)	Avicularia width (μm)	Ascopore length (μm)	Ascopore width (μm)	Mandible length (μm)	Mandible width (μm)
76.89	55.44	30.75	30.75	177.8	59.46
81.82	55.82	30.58	37.32	223.08	44.31
74.95	55.4	22.92	26.13	284.51	48.39
92.15	51.26	28.99	23.93	195.78	34.55
70.62	56.62	21.74	29.8	245.58	54.15
62.95	42.64	19.58	32.42	303.43	69.35
68.81	71.4	18.34	25.32	287.48	68
67.11	42.08	16.69	33.38		
70.17	64.92	16.21	18.48		
69.83	66.12	30.58	25.32		
50.64	39.17	21.13	20.63		
66.16	53.17	25.32	33.38		
58.35	43.79	22.29	22.92		
68.77	53.52	41.52	35.59		
66.64	50.33	31.18	43.61		
48.19	41.52	37.32	37.32		
72.49	40.55	30.84	37.32		
96.96	42.82	26.73	35.66		
89.43	57.72	29.89	35.06		
68.81	60.3	29.89	34.08		
76.2	49.38	32.09	39.04		

Rhynchozoon sp.

Zooid length (μm)	Zooid width (μm)	Avicularia length (μm)	Avicularia width (μm)
237.86	157.91	98.97	80.53
227.8	166.97	128.48	83.67
165.12	154.43	111.2	83.03
210.91	146.23	111.98	85.93
201.32	196.89	197.27	103.59
267.48	163.73	147.52	76.31
246.06	179.71	136.09	80.5
254.97	196.95	104.4	96.74
199.9	141.78	124.26	74.85
201.95	163.68	101.75	90.69

247.16	211.63	83.35	103.79
237.23	149.27	128.32	57.49
270.49	161.08	123.88	75.96
207.86	156.71	78.24	64.23
206.37	200.09	113.24	103.03
224.86	160.23	107.84	65.64
259.39	196.85	107.65	36.96
276.97	175.82		
255.91	178.67		
188	211.62		
262.69	175.73		
149.45	115.85		
196.7	280.45		
211.21	189.54		
185.58	177.1		
210.47	193.03		
247.97	191.53		
185.18	188.95		
261.4	160.55		
278.54	393.95		

Celleporaria sp.1

Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Avicularia length (μm)	Avicularia width (μm)	Mandible length (μm)	Mandible width (μm)
267.87	240.98	86.66	109.37	85.1	45.04	60	57.86
297.58	216.48	94.91	92.75	56.38	59.16	56.38	51.97
237.23	200.18	91.01	102.24	61.17	60.17	52.27	62.36
305.41	208.12	73.39	87.53	64.72	44.51	51.72	49.22
270.25	181.7	86.66	73.82	66.16	61.72		
252.55	224.54	88.19	59.78	70.32	56.94		
260.35	184.54	83.95	76.31				
296.05	163.55	92.3	93.57				
287.01	165.27	69.61	90.83				
216.73	191.58	69.72	73.39				
282.73	223.79	104.65	78.08				
350.34	193.78	81.31	90.22				
254.66	184.43	88.07	82.18				
228.08	182.28	85.28	27.58				
298.91	188.88	95.54	88.49				
308.33	247.59	84.57	88.46				
228.57	202.06	96.72	81.24				
208.16	201.03	57.49	80.23				
315.48	165.63						

Celleporaria sp.2

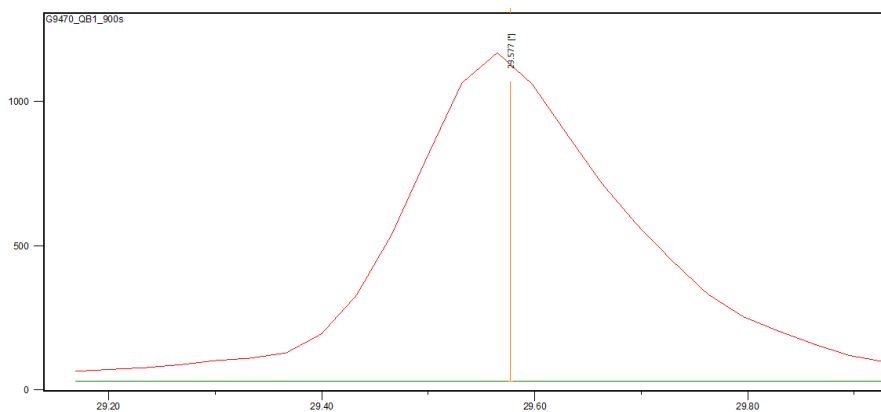
Zooid length (μm)	Zooid width (μm)	Orifice length (μm)	Orifice width (μm)	Umbo length (μm)	Umbo width (μm)
149.64	102.52	43.61	30.15	92.27	23.93
131.97	78.41	37.8	39.04	83.45	18.9
163.94	133.4	36.96	42.82	83.07	23.93
216.33	110.89	21.62	31.93	60	14.67

245.39	93.99	34.08	39.17	97.31	15.37
205.88	88.19	47.87	37.32	76.31	23.6
279.24	124.13	39.17	31.93	81.4	27.6
137.57	89.67	35.59	36.24	114.46	26.83
193.44	104.07	37.94	41.32	62.57	18.34
179.05	120.28	29.8	31.18	75.2	27.6
237.99	97.26	41.26	46.07	57.31	34.69
199.39	71.4	36.96	46.07	106.64	25.63
154.57	84.35	35.06	49	106.67	29.8
188.29	109.2	40.1	39.17	73.11	37.32
170.2	117.43	38.15	37.32	46.42	25.93
183.4	86.29	33.06	36.24	47.2	19.72
133.28	92.15	33.06	31.18	75.68	25.32
142.8	108.35	21.62	40.03	103.26	27.89
180.28	97.61	39.17	41.01	58.44	22.69
142.69	116.71	33.38	33.38	48.74	21.62
134.5	86.51	41.01	41.32	103.67	42.27
147.81	86.14	32.58	42.79		
145.6	94.1	42.27	31.18		
186.61	94.24	34.38	46.42		
208.16	89.29	42.27	34.38		
185.82	115.85	33.84	42.64		

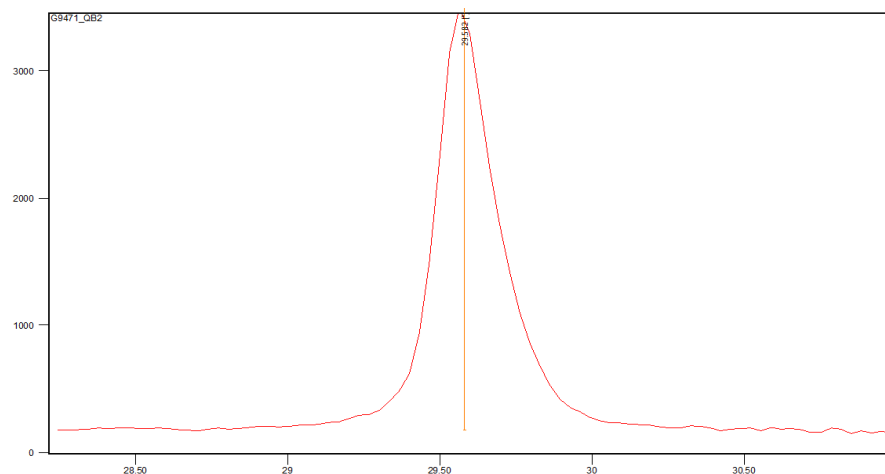
Appendix M. X-ray diffraction spectrum for Qatar Bryozoa (red line: midpoint position of the peak approx. 29.6 on the x-axis), Y-axis shows counts of peak intensity. X-axis shows the angle of diffraction (2θ)

Biflustra sp.

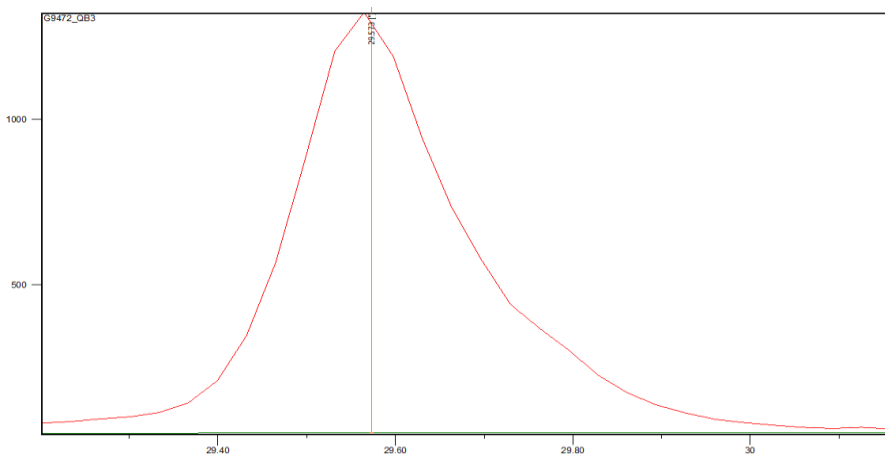
QB1



QB2

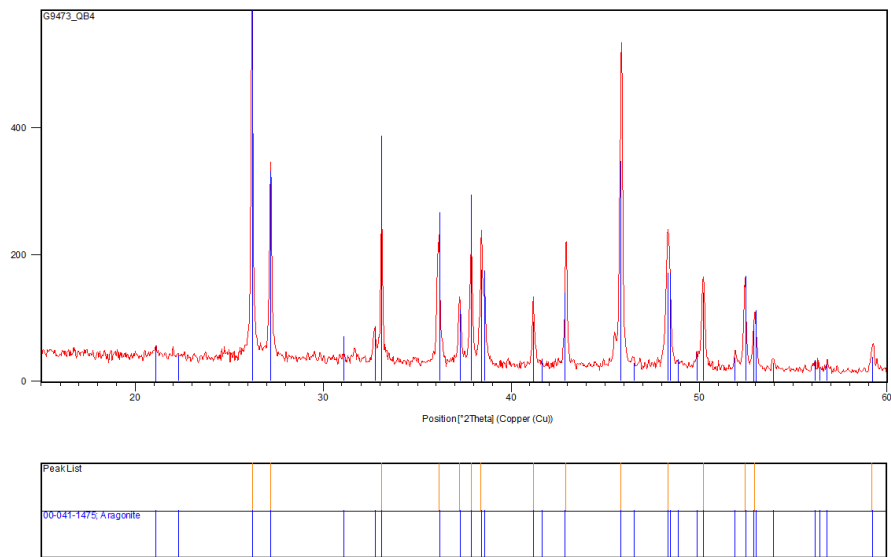


QB3



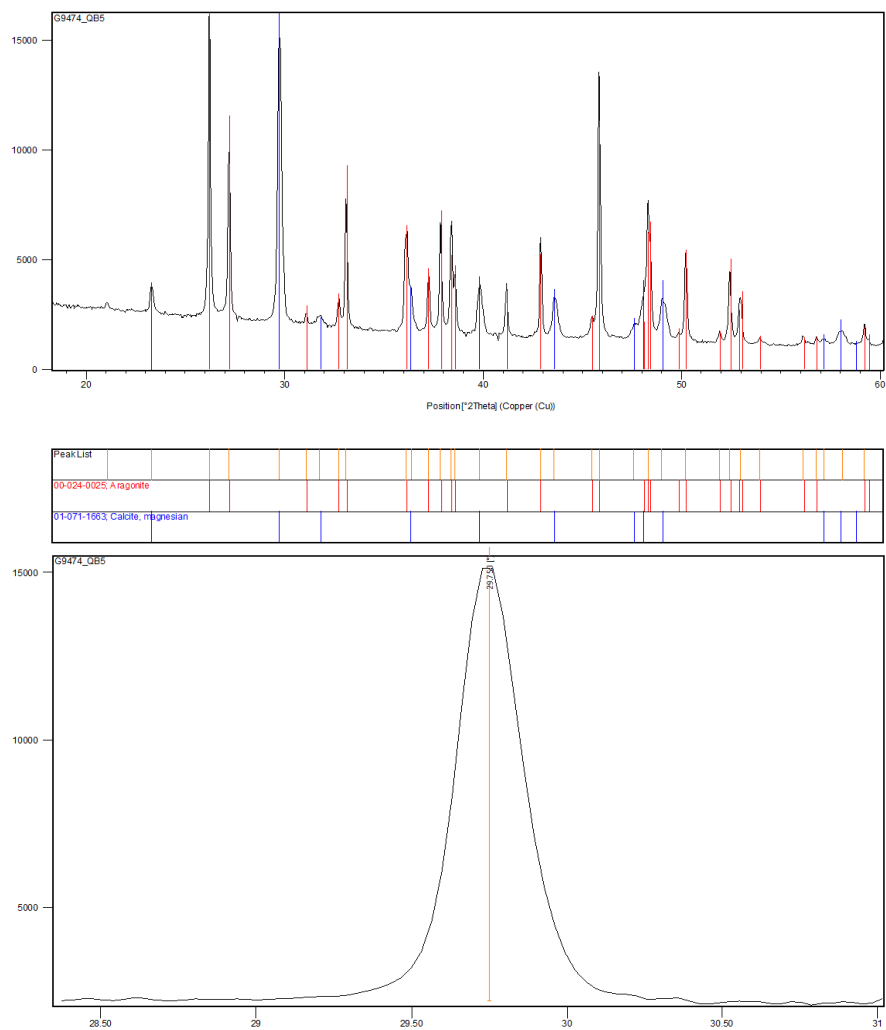
Celleporaria sp.2

QB4

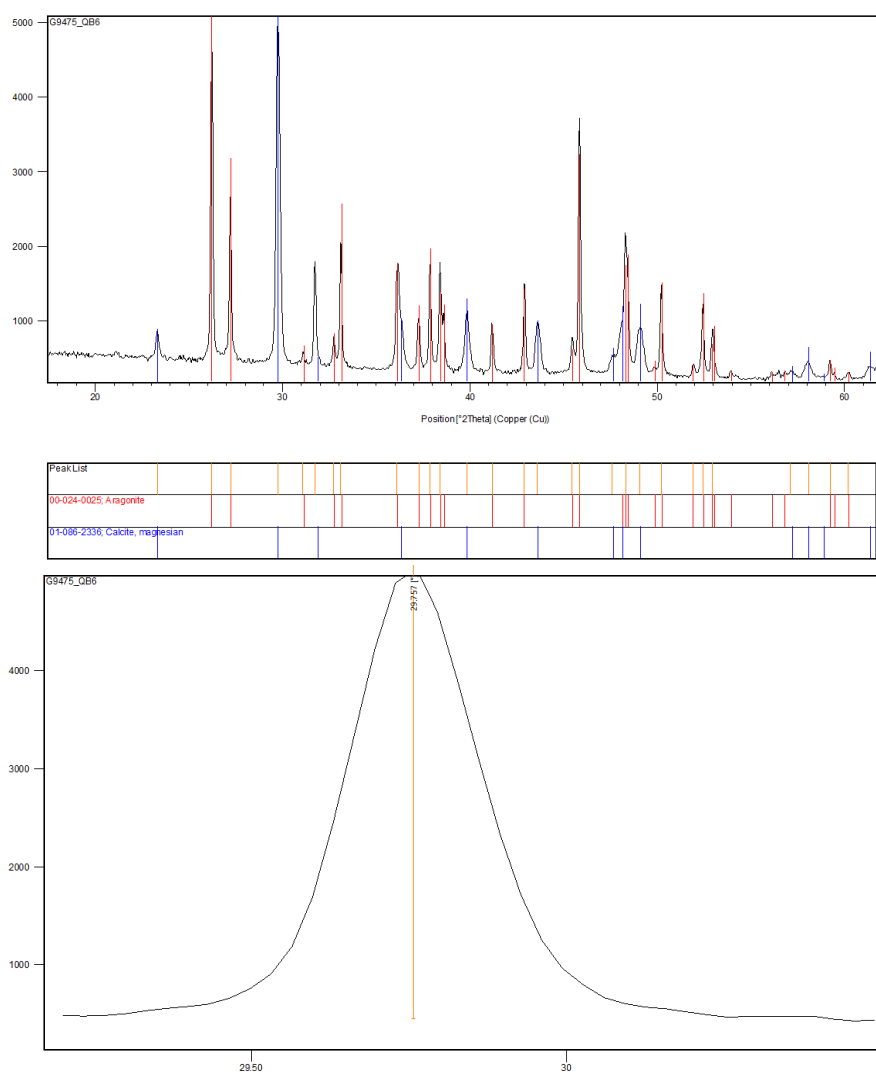


Schizoporella errata

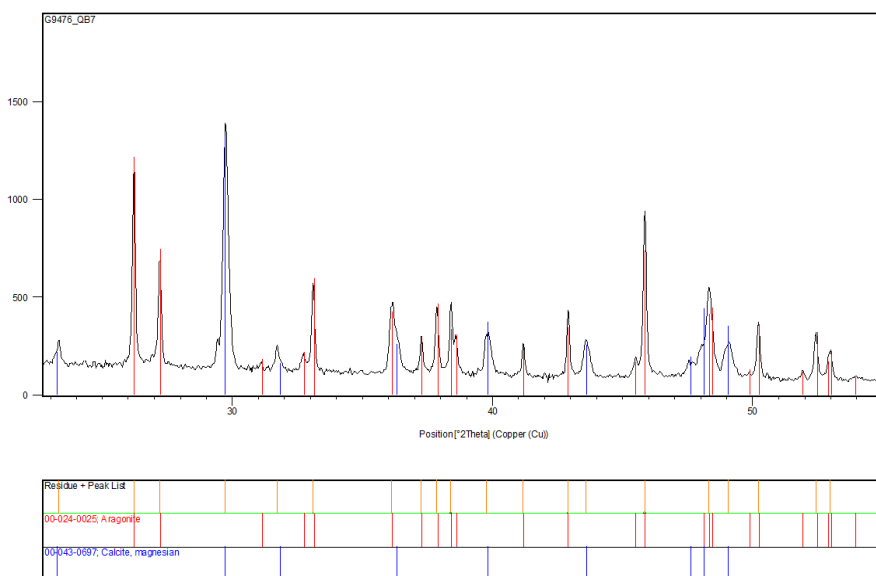
QB5

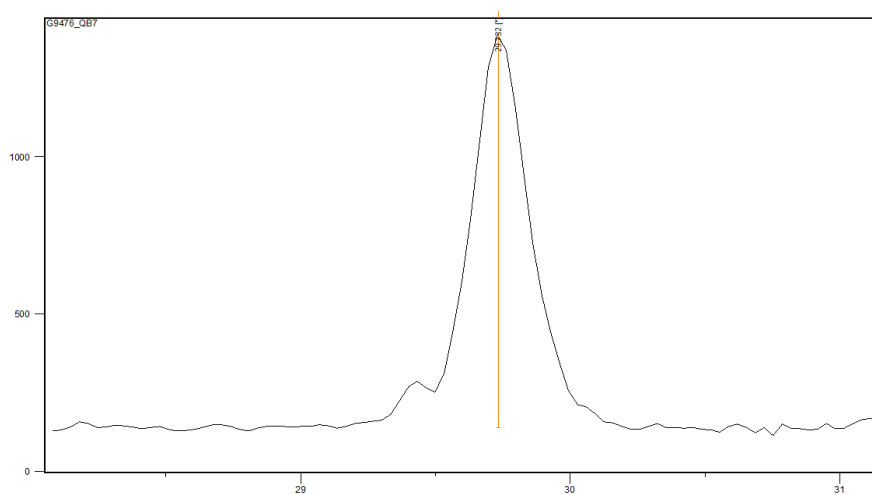


QB6



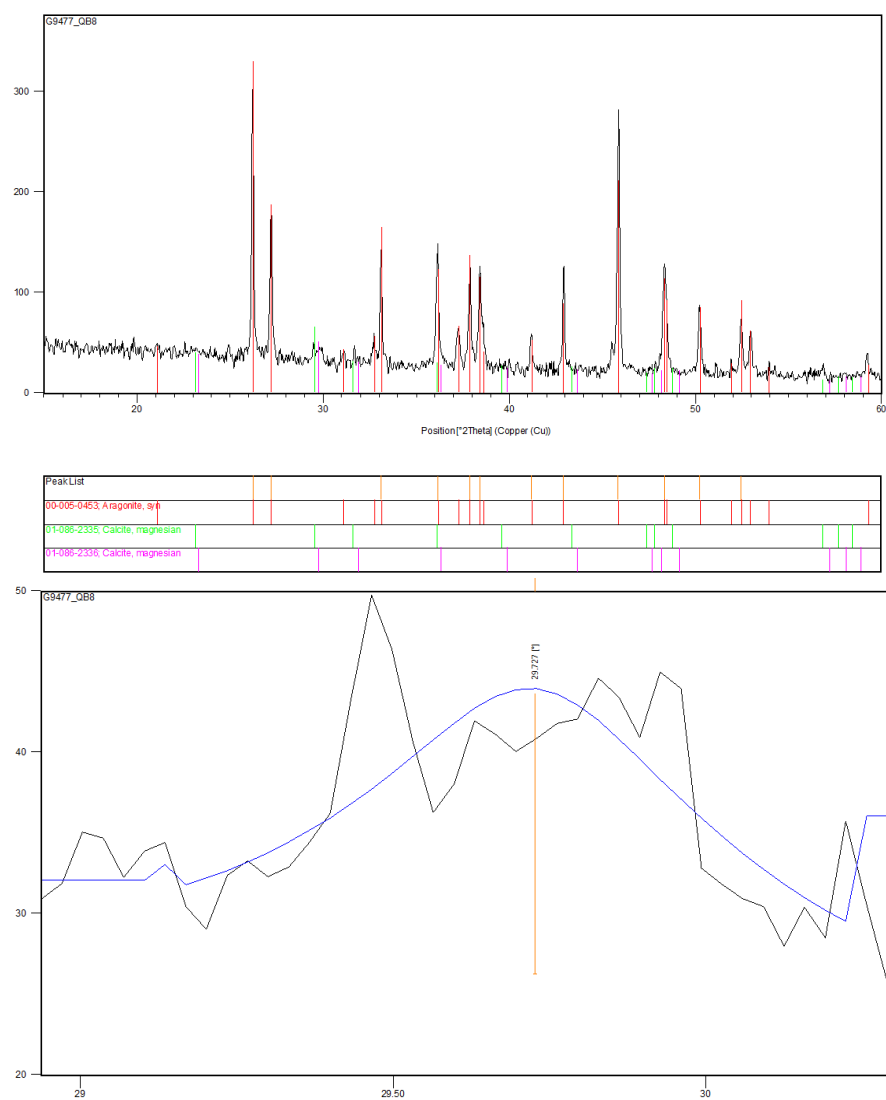
QB7



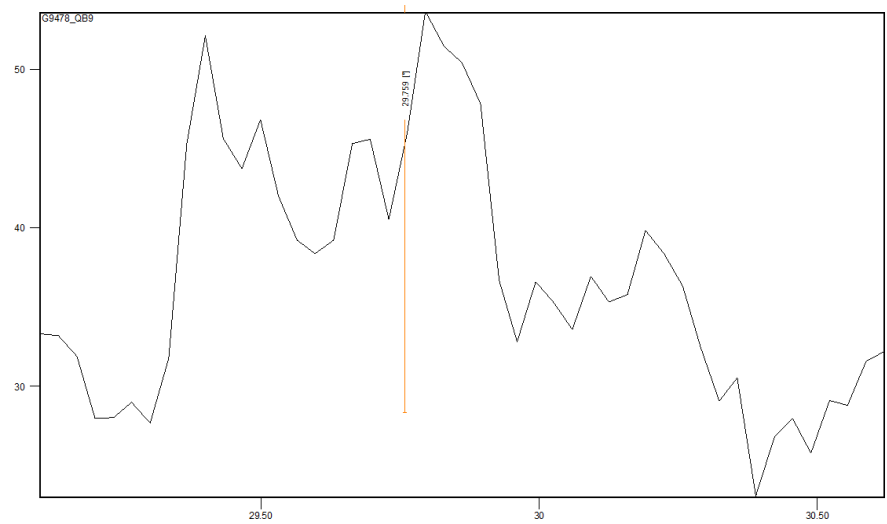
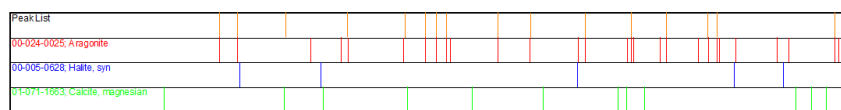
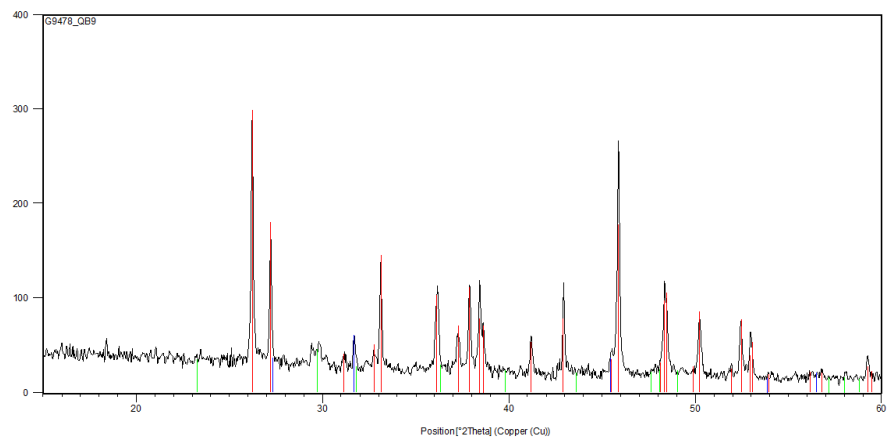


Parasmittina egyptiaca

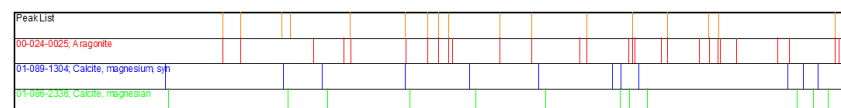
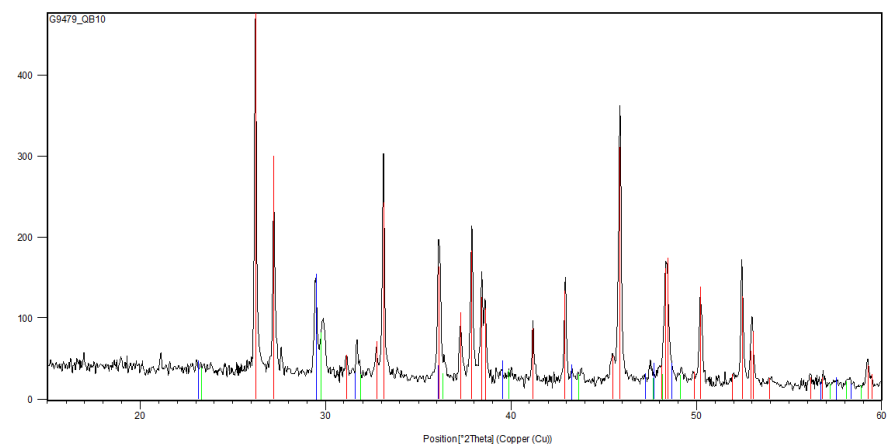
QB8

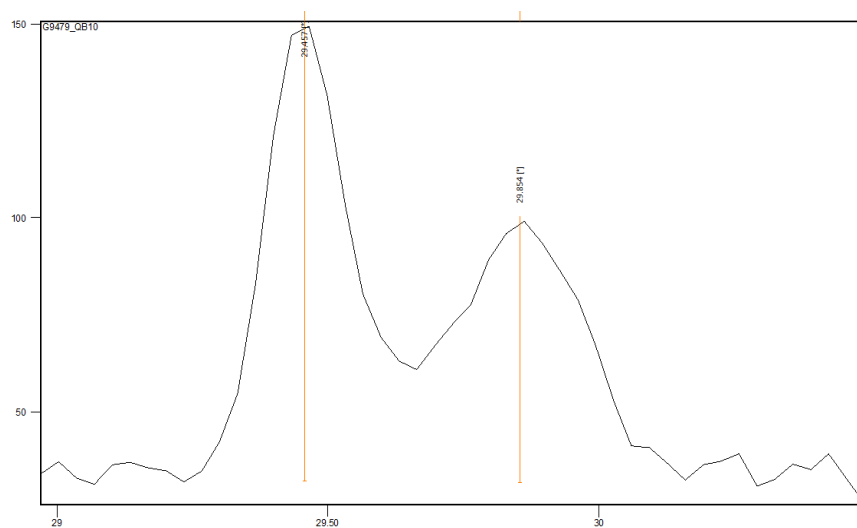


QB9



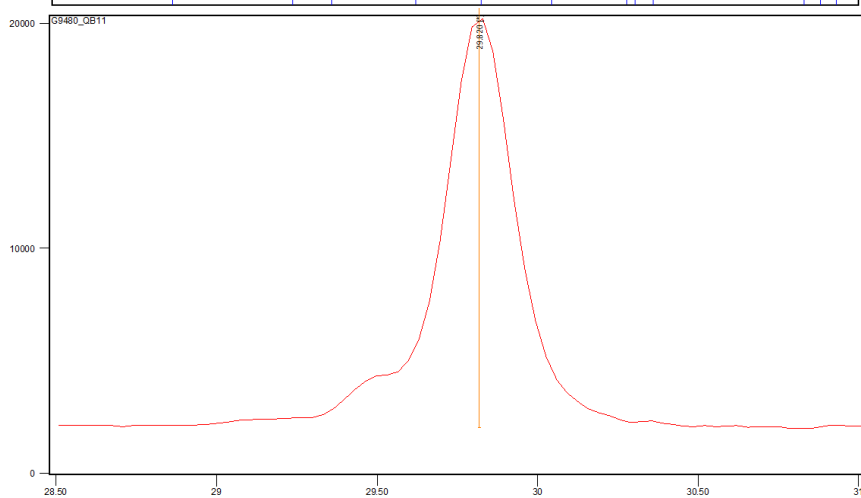
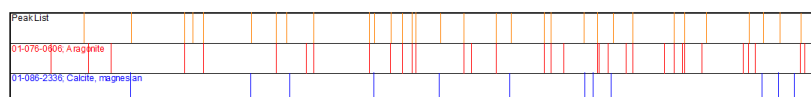
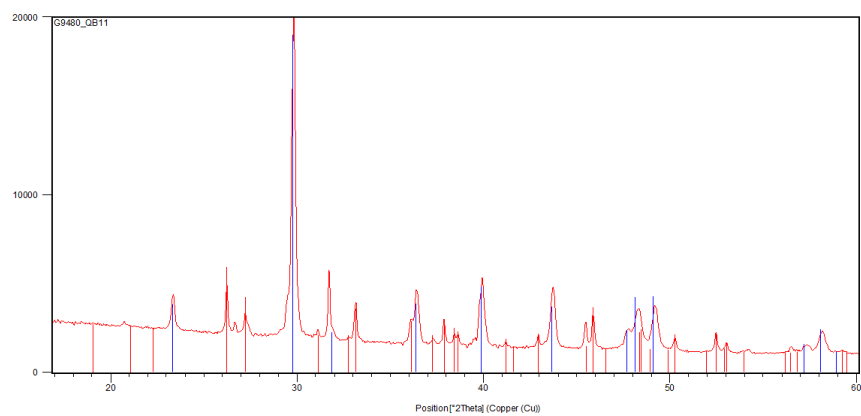
QB10



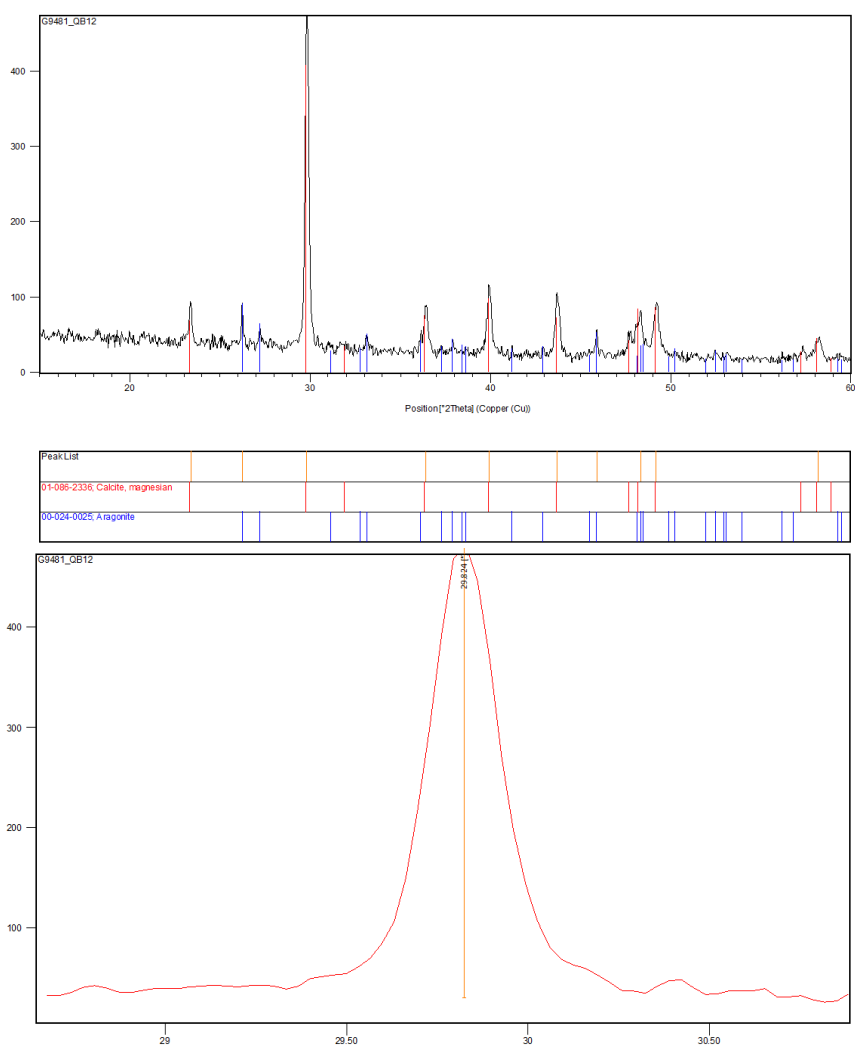


Trypostega johnsoulei

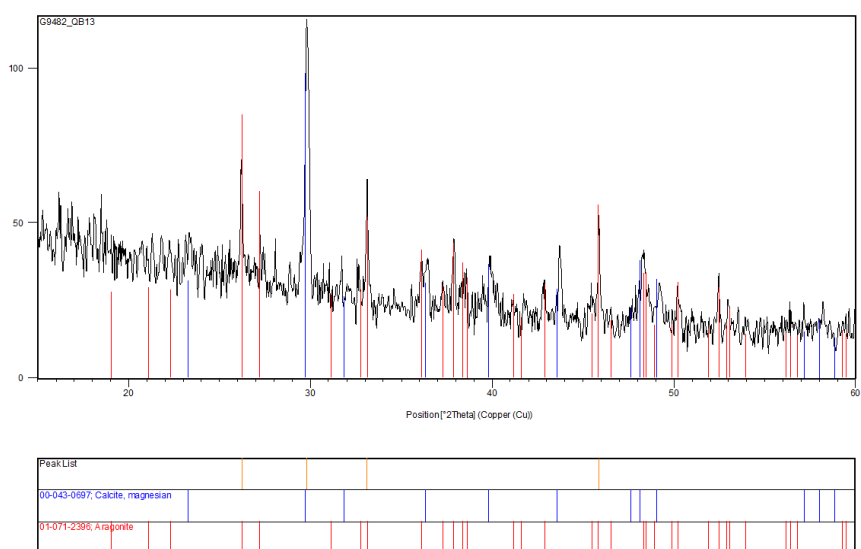
QB11

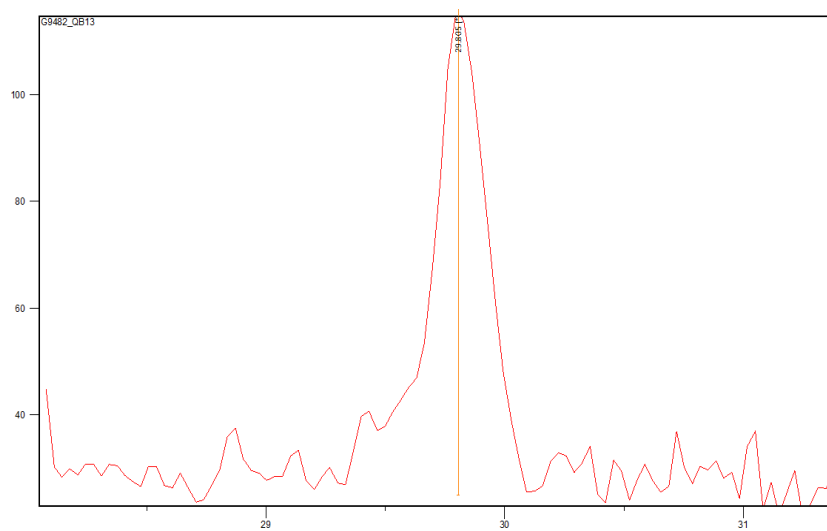


QB12



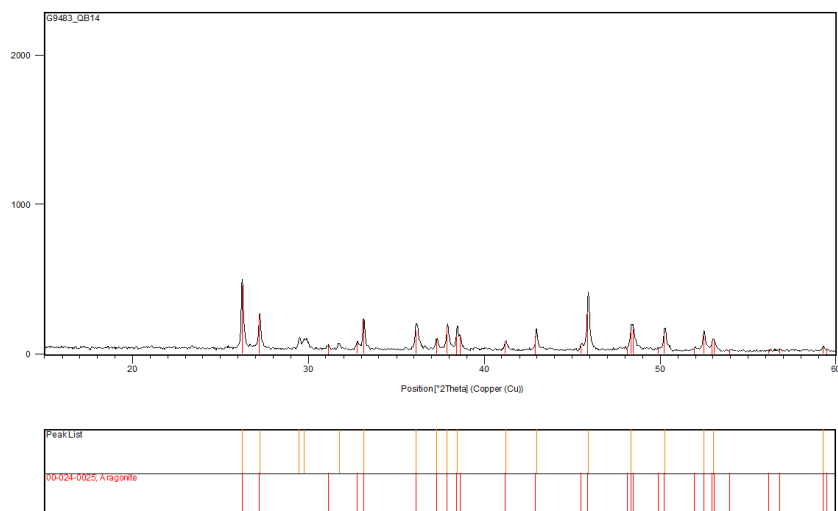
QB13





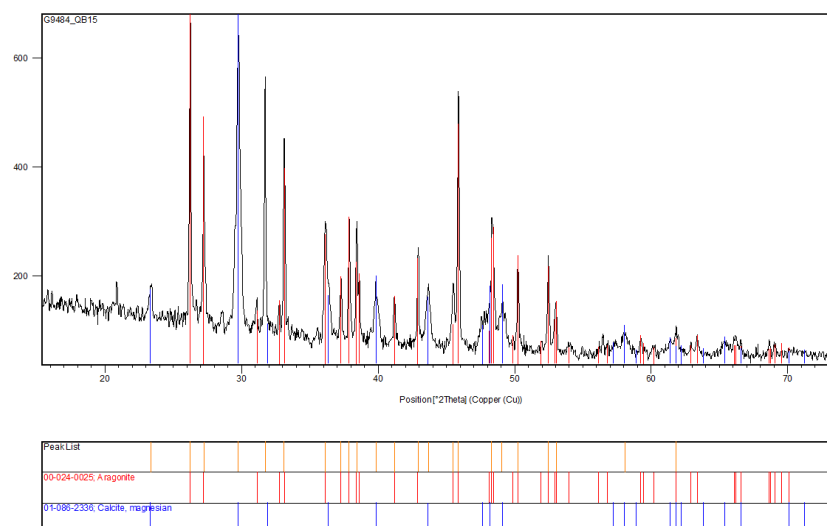
Celleporaria sp.1

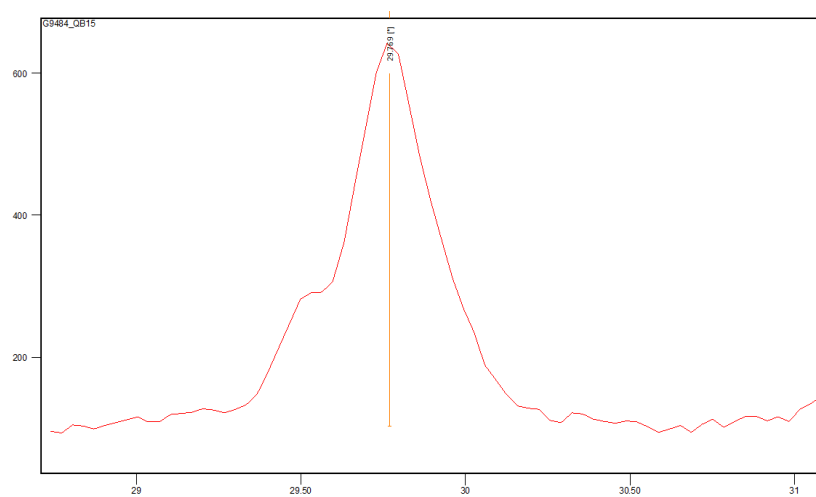
QB14



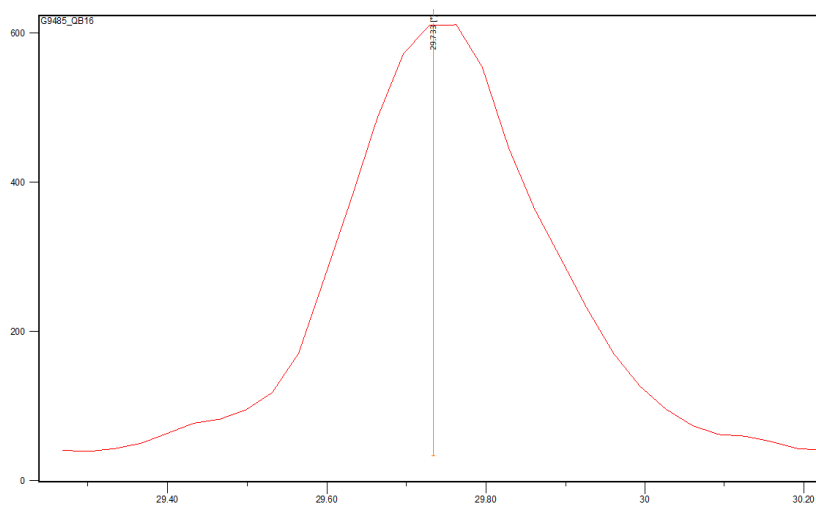
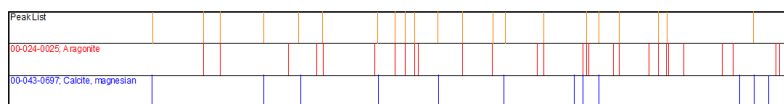
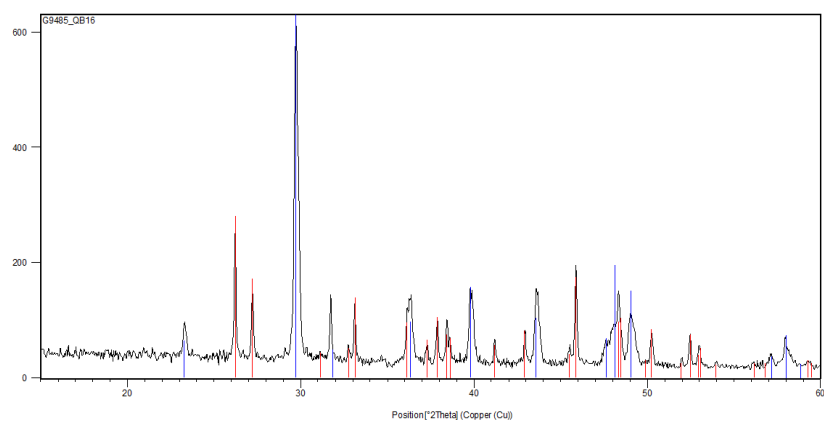
Poricella robusta

QB15

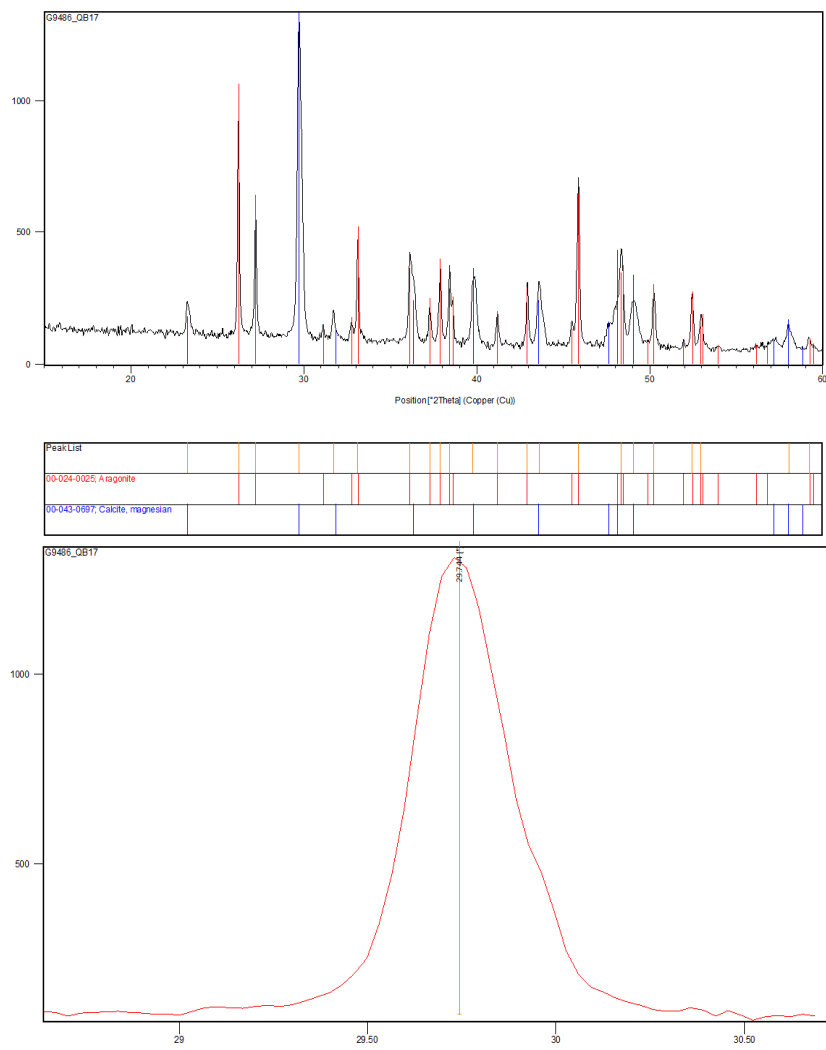




QB16

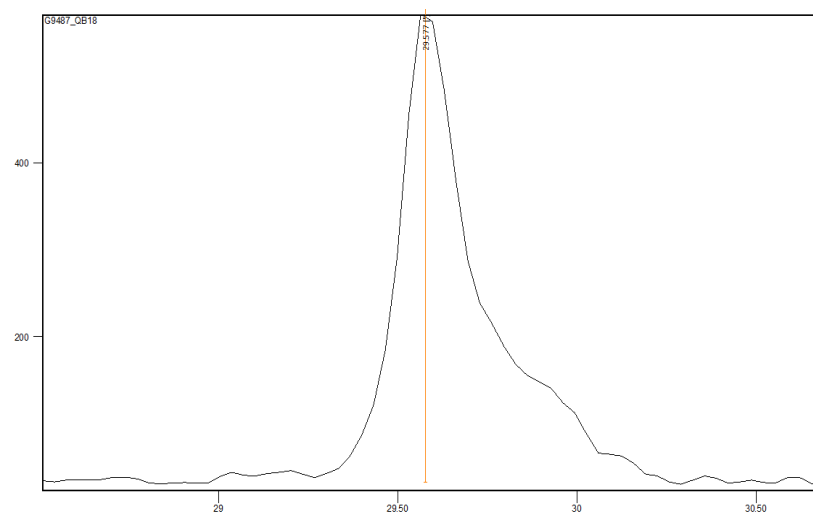


QB17

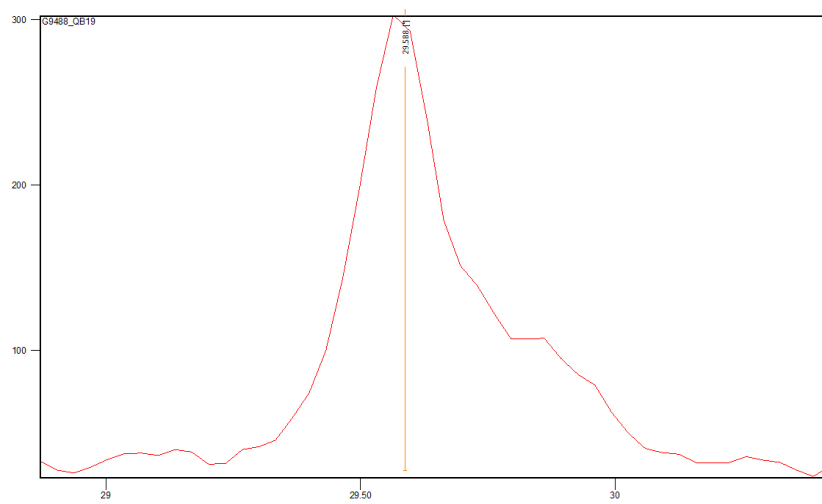


Thalamoporella granulata

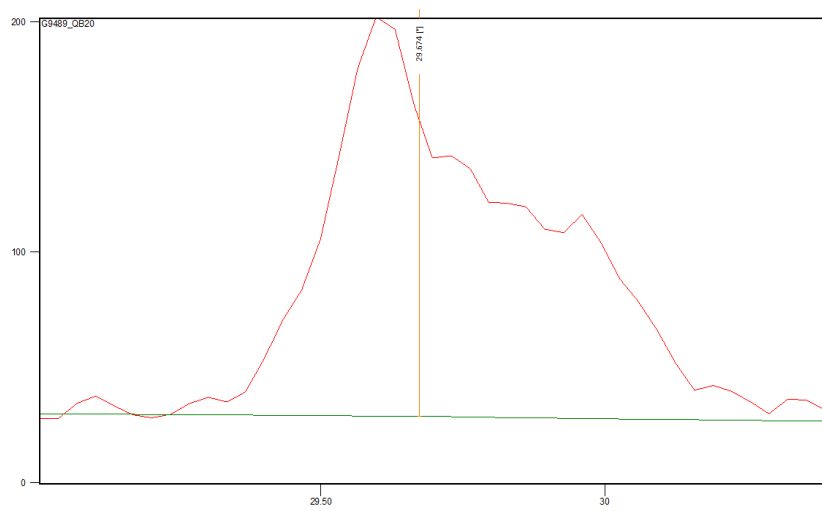
QB18



QB19

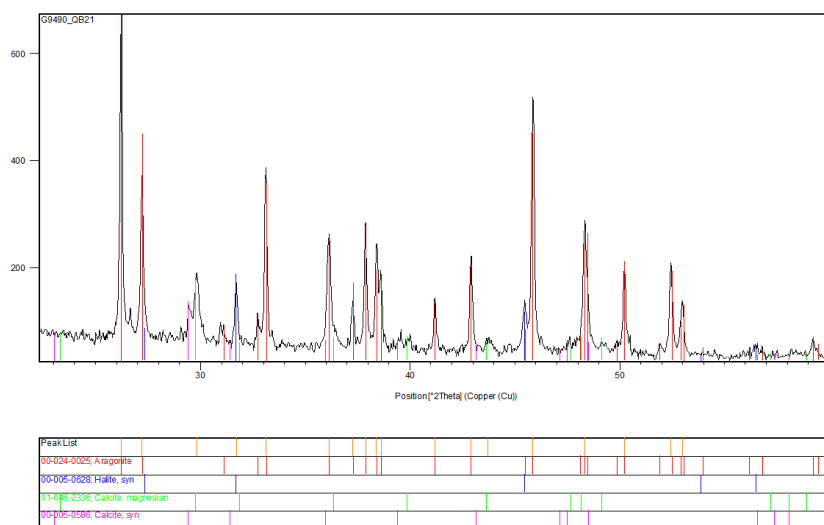


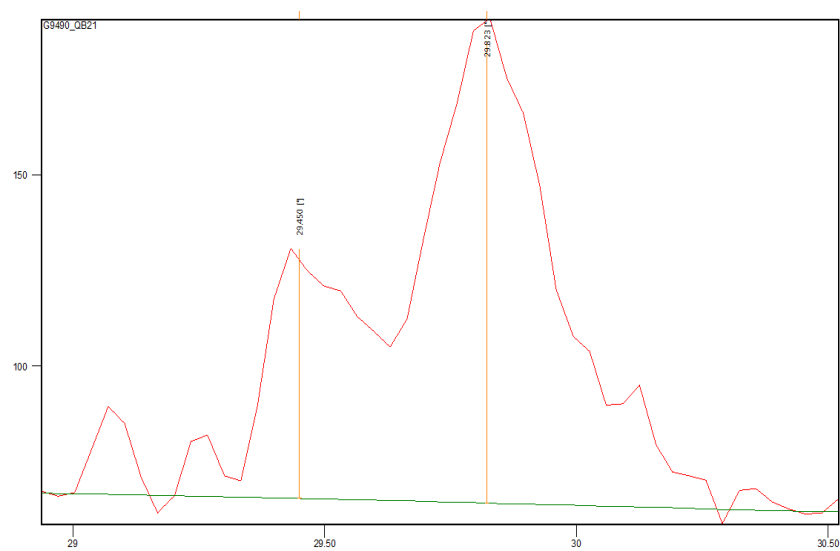
QB20



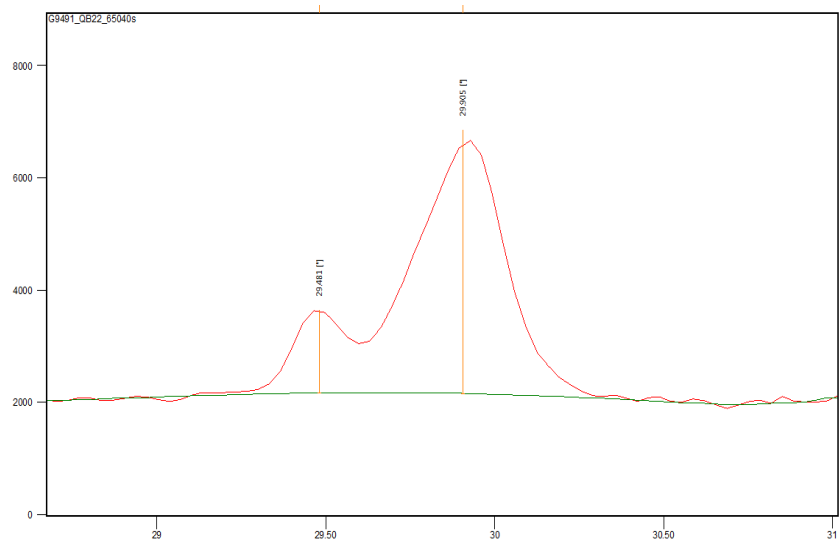
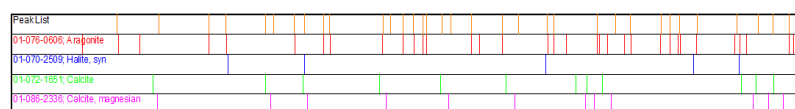
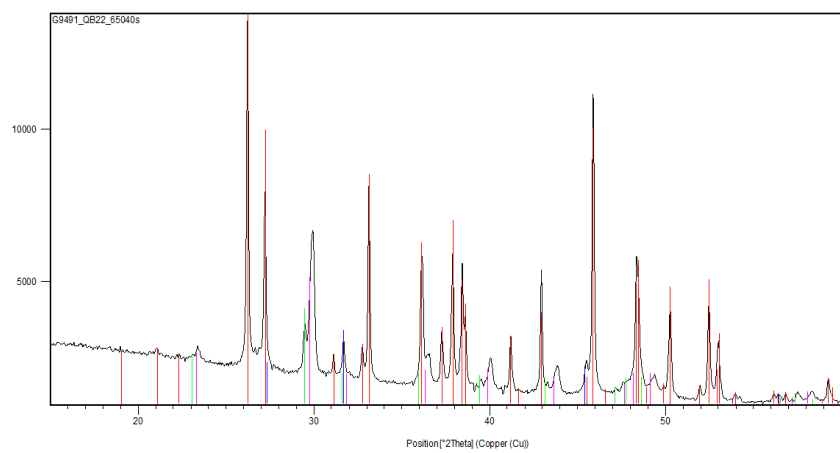
Rhynchozoon sp.

QB21

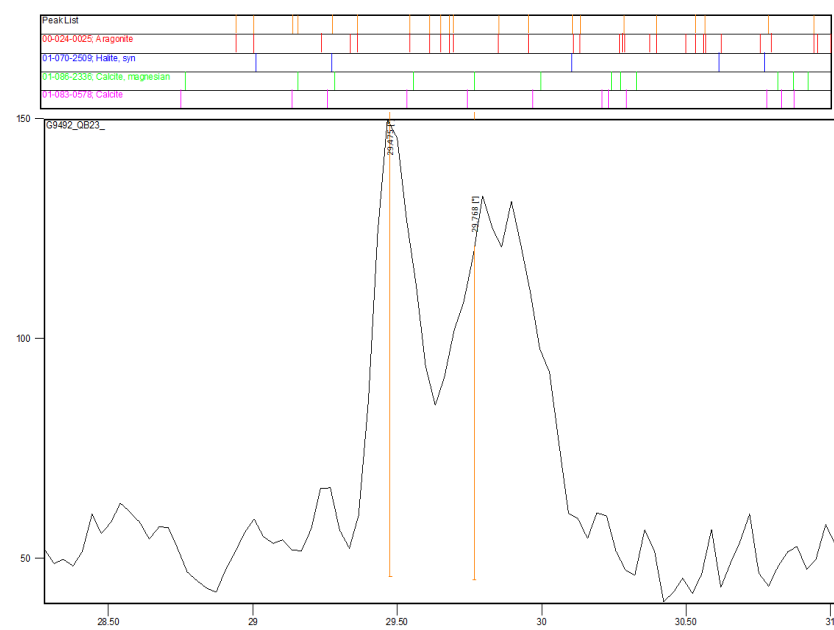
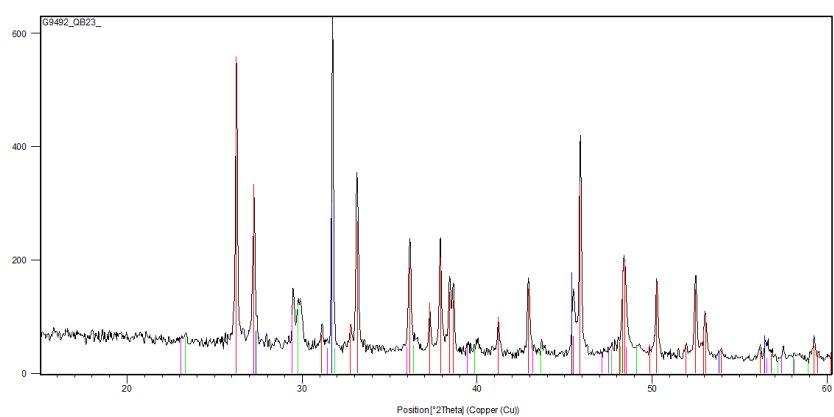




QB22



QB23



Appendix N. Calculation of the mole percent (Mol. %) of MgCO₃ in calcite for Qatar

Bryozoa

Species	Sample	Diff angle [°]	d(104) [Å]	mol frac Mg	mol % Mg	Mean	SD
<i>Biflustra</i> sp.	QB1	29.57	3.01850	0.05630	5.6	5.7	0.19659
	QB2	29.58	3.01751	0.05971	6.0		
	QB3	29.57	3.01850	0.05630	5.6		
<i>Schizoporella errata</i>	QB5	29.75	3.00065	0.11724	11.7	11.6	0.19433
	QB6	29.75	3.00065	0.11724	11.7		
	QB7	29.74	3.00164	0.11387	11.4		
<i>Parasmittina egyptiaca</i>	QB8	29.72	3.00361	0.10713	10.7	12.5	2.28429
	QB9	29.75	3.00065	0.11724	11.7		
	QB10	29.85	2.99082	0.15077	15.1		
<i>Trypostega johnsoulei</i>	QB11	29.81	2.99475	0.13739	13.7	14.0	0.38668
	QB12	29.83	2.99278	0.14408	14.4		
	QB13	29.81	2.99475	0.13739	13.7		
<i>Poricella robusta</i>	QB15	29.76	2.99966	0.12060	12.1	11.5	0.51412
	QB16	29.73	3.00262	0.11050	11.1		
	QB17	29.74	3.00164	0.11387	11.4		
<i>Thalamoporella granulata</i>	QB18	29.57	3.01850	0.05630	5.6	6.9	1.86938
	QB19	29.58	3.01751	0.05971	6.0		
	QB20	29.67	3.00856	0.09025	9.0		
<i>Rhynchozoon</i> sp.	QB21-1	29.48	3.02751	0.02555	2.6	2.7 15.1	0.52333 1.45555
	QB21-2	29.82	2.99376	0.14073	14.1		
	QB22-1	29.5	3.02551	0.03240	3.2		
	QB22-2	29.9	2.98594	0.16745	16.7		
	QB23-1	29.47	3.02852	0.02212	2.2		
	QB23-2	29.83	2.99278	0.14408	14.4		

Appendix O. Abstract of the 13th Larwood Symposium June 2015

Investigation of the biodiversity and ecology of encrusting epifauna associated with bivalve molluscs

By: Marwa Mohammed AlGhanem

Supervisors: Dr Joanne Porter, Dr William Sanderson, Dr Dan Harries

Preferred presentation medium talk

Are you a student? Yes

Key Words: *Modiolus modiolus*; biogenic reefs; epifauna

Biogenic reefs created by the Horse mussel *Modiolus modiolus* provide hard substrates in areas that would otherwise be dominated by sediment. Although *M. modiolus* a species is widespread and common, true reefs forming a distinctive habitat are much more limited in their distribution. The reefs comprise raised structures, bound together by a matrix of byssus threads which occur in various gradations of density and thickness (Walters, 2006). They provide a wide range of diverse epifaunal Communities that are classified as priority Marine Habitats (PMH's) (OSPAR, 2010). Horse mussels are efficient filter feeders capable of depleting the water column of phytoplankton, and play an important role in the transfer of nutrients from the water column into the benthos in coastal areas and estuaries (Dame et al., 1991). Reefs physically support a diverse assemblage of suspension feeders, including barnacles (e.g. *Balanus balanus*), tube worms (e.g. *Spirobranchus triqueter*), and bryozoans (e.g. *Electra pilosa*). The aim of this study is to generate a comprehensive account of the encrusting epifaunal communities (Bryozoans, Polychaete and barnacles) from reef sites throughout the range of the species (from Norway to the southern Irish Sea). This will inform understanding of size-related

epifaunal succession, based on epifaunal abundances and community composition associated with this PMH.



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References

- Dame, R., Dankers, N., Prins, T., Jongsma, H., Smaal, A., 1991, the influence of mussel beds on nutrients in the Western Wadden Sea and Eastern Scheldt Estuaries, 14, 130–138
- OSPAR, 2010, Background Document for *Modiolusmodiolus* beds, OSPAR Commission, UK
- Walters, T.H., 2006, *Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata, [Online], available: <http://www.marlin.ac.uk/habitat ecology.php?habitatid=137&code=> [accessed 31/03/2015]

Appendix P. Abstract of the MASTS Annual Meeting 19-21 October 2016

Investigation of the biodiversity and ecology of encrusting epifauna associated with horse mussel *Modiolus modiolus* in the North-East Atlantic

Marwa Mohammed AlGhanem¹, Dr Joanne Porter², Dr William Sanderson³, Dr Dan Harries⁴

¹Marwa Mohammed AlGhanem, School of Life Sciences, Heriot Watt University, Edinburgh, Scotland, [mma60@hw.ac.uk](mailto:mmma60@hw.ac.uk)

²Dr. Joanne Porter, International Centre Island Technology, Heriot Watt University, Orkney Campus

³Dr. William Sanderson, School of Life Sciences, Heriot Watt University, Edinburgh, Scotland

⁴Dr. Dan Harries, School of Life Sciences, Heriot Watt University, Edinburgh, Scotland

Area being submitted to: General science session.

Are you a student? Yes

Preferred presentation medium: oral

Key Words: *Modiolus modiolus*; biogenic reefs; epifauna

Biogenic reefs created by the horse mussel *Modiolus modiolus* provide hard substrates in areas that would otherwise be dominated by sediment. Although *M. modiolus* a species is widespread and common, dense reefs of *M. modiolus* form a distinctive habitat are much more limited in their distribution. The reefs comprise raised structures, bound together by a matrix of byssus threads which occur in various densities and thicknesses (Walters, 2006). Reefs support a wide range of infauna and epifauna and therefore classified as Priority Marine Habitats for conservation in the NE Atlantic (PMH's) (OSPAR, 2010). Reefs physically support a diverse assemblage of suspension feeders, including encrusting species such as barnacles, tube worms, and bryozoans that to date have been poorly described. The aim of this study is to investigate the encrusting epifauna on different horse mussel shell regions and on shells of different sizes across eight sites throughout the NE Atlantic. The encrusting epifaunal community was recorded, species identity confirmed with selected SEM imagery and the species abundance data subjected to standard multivariate analyses to give an

understanding of the community complexity of horse mussel shell epifauna, and relate the community of epifaunal organisms to the micro-environmental and bio-geographic context.



References

- OSPAR, 2010, Background Document for *Modiolus modiolus* beds, OSPAR Commission, UK
- Walters, T.H., 2006, *Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata, [Online], available: <http://www.marlin.ac.uk/habitat ecology.php?habitatid=137&code=> [accessed 31/03/2015]

Appendix Q. CTD data of pearl oyster beds November 2015

Station	dd-mm- yyyy, hh:mm:ss.sss	Longitude [degrees_east]	Latitude [degrees_north]	Bot. Depth [m]	Depth [salt water, m]	Temperature [ITS-90, deg C]	Salinity, Practical [PSU]	Density [sigma-t, kg/m^3]	Oxygen, SBE 43 [mg/l]	Oxygen, SBE 43 [% saturation]	Fluorescence, WET Labs ECO-AFL/FL [mg/m^3]	Turbidity, WET Labs ECO [NTU]
1	5-11-2015, 11:27:31.000	52.38233	25.37617	17	1	30.3727	40.1365	25.4531	5.7588	95.566	0.796	0.5845
					2	30.3809	40.136	25.4499	5.7544	95.505	0.8837	1.0491
					3	30.382	40.1361	25.4496	5.7589	95.581	0.8198	1.0489
					4	30.3804	40.1364	25.4503	5.781	95.946	0.8652	1.0361
					5	30.3798	40.1369	25.451	5.7621	95.632	0.952	1.0273
					6	30.3782	40.1375	25.4519	5.7615	95.619	0.9466	1.0175
					7	30.3793	40.1373	25.4514	5.759	95.579	0.9244	1.0125
					8	30.374	40.1369	25.453	5.7761	95.856	0.9623	1.0258
					9	30.3631	40.1369	25.4568	5.7546	95.481	0.9782	1.0385
					10	30.3518	40.1381	25.4616	5.7341	95.126	1.0012	1.0372
					11	30.3339	40.1423	25.471	5.7096	94.694	0.9735	1.04
					12	30.3233	40.1467	25.4781	5.6391	93.513	1.0068	1.0553
					13	30.3213	40.1525	25.4832	5.6343	93.433	1.0552	1.0657
					14	30.3224	40.1592	25.4878	5.4776	90.84	0.8736	1.0305
					15	30.3235	40.1597	25.4878	5.4697	90.71	0.7508	1.0021
					16	30.3228	40.1593	25.4877	5.4526	90.425	0.7292	1.015
1	5-11-2015, 14:59:14.000	52.38433	25.37417	16	1	30.3628	40.1791	25.4886	5.4998	91.275	0.9544	1.4644
					2	30.3635	40.1796	25.4887	5.5245	91.686	0.9307	1.0942
					3	30.3621	40.1801	25.4896	5.5178	91.573	1.0257	1.0814
					4	30.3638	40.1797	25.4887	5.5254	91.701	0.9886	1.0763
					5	30.3692	40.1791	25.4864	5.5345	91.86	0.9751	1.0845
					6	30.369	40.1796	25.4868	5.5354	91.876	0.9069	1.1078
					7	30.3702	40.1773	25.4847	5.5595	92.275	0.9811	1.0848
					8	30.3638	40.176	25.4859	5.5562	92.211	0.9779	1.0993
					9	30.3751	40.1836	25.4877	5.564	92.361	0.9599	1.0792
					10	30.4063	40.2044	25.4924	5.5234	91.743	0.9661	1.0792
					11	30.4394	40.2279	25.4985	5.4679	90.879	0.9775	1.0942
					12	30.4577	40.241	25.5019	5.4196	90.11	0.9295	1.1125
					13	30.4801	40.2577	25.5066	5.4085	89.964	1.0025	1.0918

					14	30.5166	40.2828	25.5126	5.3243	88.627	1.0002	1.1148
					15	30.525	40.2881	25.5137	5.3216	88.596	0.918	1.1039
1	5-11-2015, 21:00:50.000	52.38383	25.37383	16	1	30.4006	40.3214	25.5824	5.4915	91.263	0.6822	1.0502
					2	30.4049	40.3214	25.5808	5.4988	91.39	0.7042	1.0664
					3	30.4033	40.3212	25.5812	5.5042	91.478	0.667	1.0449
					4	30.4027	40.3211	25.5814	5.5187	91.718	0.7071	1.0384
					5	30.4025	40.3206	25.5811	5.5405	92.08	0.7169	1.0457
					6	30.4003	40.3205	25.5818	5.5353	91.991	0.7282	1.0534
					7	30.4023	40.3208	25.5813	5.5198	91.735	0.7078	1.0565
					8	30.4022	40.3209	25.5814	5.5137	91.634	0.6862	1.0482
					9	30.4005	40.3208	25.5819	5.524	91.802	0.7125	1.0348
					10	30.3993	40.3204	25.582	5.5152	91.655	0.7123	1.0973
					11	30.3979	40.3204	25.5825	5.5276	91.859	0.6877	1.0412
					12	30.3982	40.3202	25.5822	5.4974	91.357	0.6879	1.0725
					13	30.395	40.3194	25.5828	5.5278	91.857	0.7021	1.0413
					14	30.3975	40.3194	25.582	5.541	92.081	0.7057	1.0454
					15	30.3973	40.3194	25.582	5.5438	92.126	0.7296	1.0501
2	6-11-2015, 03:08:05.000	52.33533	25.40833	28	16	30.3931	40.3187	25.583	5.5334	91.947	0.7271	1.0427
					1	30.1811	40.0372	25.4454	5.6796	93.917	0.5922	1.0254
					2	30.1808	40.0371	25.4454	5.6961	94.189	0.5983	0.9979
					3	30.1857	40.0376	25.444	5.6888	94.075	0.5804	0.9934
					4	30.1949	40.0377	25.441	5.6824	93.983	0.5882	1.0034
					5	30.1941	40.0381	25.4415	5.6838	94.005	0.6004	1.0041
					6	30.1908	40.0379	25.4425	5.6933	94.158	0.5986	0.9989
					7	30.1873	40.0387	25.4444	5.6778	93.896	0.5862	0.9946
					8	30.1947	40.0383	25.4415	5.692	94.142	0.5925	0.9956
					9	30.1937	40.0387	25.4421	5.6835	94.001	0.6055	0.9957
					10	30.1898	40.0403	25.4447	5.6844	94.01	0.5802	0.9888
					11	30.1991	40.0629	25.4584	5.6968	94.242	0.5861	1.0141
					12	30.235	40.1217	25.4901	5.6812	94.066	0.5884	1.0062
					13	30.2244	40.1487	25.5141	5.6772	93.998	0.5887	1.0165
					14	30.2452	40.1781	25.5289	5.5952	92.686	0.6699	1.0112
					15	30.2869	40.2083	25.5371	5.6577	93.799	0.7252	1.0137
					16	30.2955	40.2199	25.5428	5.6731	94.072	0.7427	1.0131
					17	30.3085	40.2498	25.5607	5.6843	94.293	0.7568	1.0099
					18	30.3142	40.3465	25.6314	5.6777	94.242	0.7919	1.0281

					19	30.3375	40.4868	25.7288	5.5905	92.901	0.8625	0.9986
					20	30.3709	40.5679	25.778	5.3907	89.667	0.9029	1.0371
					21	30.3758	40.5965	25.7979	5.3282	88.649	0.8823	1.0643
					22	30.4071	40.6588	25.8337	5.3287	88.732	0.825	1.1257
					23	30.4259	40.6918	25.8519	5.2327	87.175	0.8013	1.1339
					24	30.4323	40.7104	25.8637	5.2108	86.827	0.7943	1.1456
					25	30.4326	40.7246	25.8743	5.1791	86.305	0.8119	1.2133
					26	30.4329	40.7235	25.8733	5.1673	86.109	0.7387	1.2452
					27	30.4333	40.7227	25.8726	5.169	86.139	0.7414	1.2499
3	6-11-2015, 05:31:33.000	52.048	25.513	24	28	30.4335	40.7274	25.876	5.1595	85.981	0.8496	1.3441
					1	30.0611	40.3034	25.6873	5.6692	93.704	0.5549	1.1919
					2	30.0583	40.3035	25.6884	5.6486	93.36	0.6013	1.1682
					3	30.0528	40.3031	25.69	5.6663	93.645	0.6478	1.1802
					4	30.0397	40.3015	25.6933	5.6769	93.8	0.7023	1.1791
					5	30.0357	40.3017	25.6949	5.6684	93.653	0.8198	1.1575
					6	30.0268	40.3046	25.7002	5.6873	93.953	0.8569	1.1879
					7	30.024	40.3211	25.7136	5.6684	93.646	0.9807	1.1852
					8	30.0248	40.3726	25.752	5.5925	92.42	1.0947	1.2028
					9	30.0313	40.4075	25.776	5.4889	90.733	1.1322	1.2227
					10	30.0389	40.4257	25.787	5.4002	89.287	1.1826	1.2206
					11	30.0412	40.4358	25.7938	5.3278	88.098	1.0293	1.2055
					12	30.047	40.4453	25.799	5.2731	87.206	0.9138	1.226
					13	30.0498	40.4529	25.8037	5.2023	86.043	0.7699	1.197
					14	30.0512	40.4573	25.8065	5.1638	85.409	0.6061	1.1534
4	6-11-2015, 07:06:29.000	52.01333	25.553	28	1	30.3342	40.0827	25.4261	5.7575	95.458	0.4141	1.0863
					2	30.2439	40.0744	25.4514	5.7785	95.667	0.3883	1.0844
					3	30.1521	40.0726	25.4821	5.756	95.155	0.4863	1.1049
					4	30.1351	40.0751	25.4899	5.7889	95.675	0.5711	1.1558
					5	30.113	40.074	25.4968	5.7991	95.81	0.6614	1.1667
					6	30.0978	40.0762	25.5037	5.8005	95.811	0.7426	1.1756
					7	30.084	40.0756	25.5081	5.7987	95.759	0.854	1.2214
					8	30.0691	40.0754	25.513	5.798	95.725	0.9337	1.2239
					9	30.0703	40.0819	25.5176	5.7858	95.529	1.0524	1.2094
					10	30.0671	40.0879	25.5232	5.7814	95.454	1.102	1.1908
					11	30.0679	40.0964	25.5293	5.7443	94.848	1.2008	1.2306

					12	30.068	40.1032	25.5344	5.7174	94.408	1.244	1.2251
					13	30.0722	40.1096	25.5377	5.6946	94.041	1.2568	1.2445
					14	30.0806	40.1207	25.5431	5.693	94.032	1.2103	1.2568
					15	30.1226	40.1766	25.5705	5.6564	93.519	1.246	1.2577
					16	30.1391	40.2192	25.5969	5.2274	86.469	1.4792	1.4205
					17	30.1155	40.2445	25.6241	5.2032	86.048	1.3618	1.4769
					18	30.0971	40.2598	25.642	5.2378	86.603	1.3068	1.4354
					19	30.102	40.3603	25.7159	5.2374	86.651	1.3093	1.4798
					20	30.1194	40.4505	25.7777	5.0383	83.421	1.1448	1.6311
					21	30.1282	40.4964	25.8091	4.97	82.323	1.081	1.7371
					22	30.1346	40.5344	25.8355	4.9266	81.63	1.084	1.7946
					23	30.1351	40.5662	25.8592	4.9285	81.675	1.0252	1.7859
					24	30.1343	40.6059	25.8893	4.9341	81.784	1.0425	1.8173
					25	30.1163	40.6912	25.9598	4.9662	82.332	0.969	1.8682
					26	30.1081	40.7045	25.9727	4.9745	82.466	0.9465	2.1326
					27	30.1057	40.7116	25.9788	4.9574	82.183	0.9383	2.5119
					28	30.1046	40.7137	25.9808	4.9487	82.037	0.9788	2.9538
5	6-11-2015, 10:49:35.000	51.86767	25.75467	22	1	30.5939	39.4396	24.852	5.8615	97.235	0.393	1.0346
					2	30.5746	39.4378	24.8575	5.858	97.146	0.4544	1.013
					3	30.259	39.4294	24.9614	5.8941	97.257	0.4551	1.0775
					4	30.0778	39.4353	25.0289	5.9149	97.325	0.5305	1.0771
					5	30.0158	39.4351	25.0502	5.9781	98.267	0.6049	1.1085
					6	29.9735	39.4334	25.0636	5.9801	98.233	0.6591	1.1624
					7	29.9396	39.432	25.0743	5.9946	98.419	0.7395	1.1663
					8	29.9186	39.4305	25.0804	5.9913	98.331	0.7623	1.1724
					9	29.8978	39.4321	25.0888	5.9731	98	0.8083	1.1753
					10	29.8831	39.4338	25.0951	5.9448	97.514	0.909	1.1924
					11	29.8705	39.4331	25.099	5.9212	97.108	1.0179	1.1866
					12	29.8618	39.4332	25.1021	5.8779	96.384	1.0718	1.2059
					13	29.8578	39.4344	25.1044	5.83	95.594	1.1794	1.217
					14	29.8549	39.4348	25.1056	5.7851	94.853	1.2824	1.2056
					15	29.841	39.434	25.1098	5.7622	94.457	1.2897	1.2205
					16	29.8359	39.4349	25.1123	5.725	93.839	1.3279	1.2178
					17	29.8342	39.4354	25.1132	5.7114	93.615	1.3407	1.2704
					18	29.8326	39.4363	25.1145	5.6862	93.199	1.3554	1.3362
					19	29.8326	39.4366	25.1147	5.6741	93.002	1.3402	1.3376

					20	29.8333	39.4366	25.1144	5.6451	92.527	1.3233	1.4007
					21	29.8341	39.4361	25.1138	5.6312	92.301	1.3245	1.5206
6	6-11-2015, 12:14:38.000	51.88233	25.73233	24	1	30.337	39.4715	24.9659	5.9754	98.742	0.7766	1.1473
					2	30.3254	39.4699	24.9687	5.9701	98.637	0.7716	1.19
					3	30.2934	39.4666	24.9774	5.992	98.946	0.7776	1.1957
					4	30.1922	39.46	25.0076	5.9963	98.855	0.8041	1.1851
					5	30.0762	39.4628	25.05	6.0718	99.918	0.9391	1.2648
					6	30.0401	39.4609	25.0612	6.0833	100.05	0.9784	1.3088
					7	30.0077	39.4643	25.075	6.0723	99.82	0.9963	1.3076
					8	29.9643	39.461	25.0875	6.0398	99.216	1.0984	1.3513
					9	29.9449	39.461	25.0942	6.0338	99.086	1.1651	1.3556
					10	29.9325	39.4635	25.1004	5.9529	97.74	1.293	1.3773
					11	29.9266	39.4682	25.106	5.9035	96.922	1.4295	1.348
					12	29.9197	39.4692	25.1091	5.8584	96.173	1.4799	1.3663
					13	29.9154	39.4693	25.1106	5.7717	94.742	1.6226	1.3959
					14	29.9117	39.4699	25.1124	5.7444	94.289	1.6178	1.4415
					15	29.9091	39.4702	25.1135	5.6854	93.316	1.5923	1.4554
					16	29.9047	39.4699	25.1149	5.6587	92.872	1.4956	1.4842
					17	29.9012	39.4695	25.1157	5.5828	91.621	1.3792	1.549
					18	29.9012	39.4693	25.1156	5.5595	91.239	1.2292	1.6194
					19	29.9011	39.469	25.1154	5.5782	91.544	1.2393	1.65
					20	29.9013	39.4691	25.1154	5.5529	91.13	1.18	1.6997
					21	29.9015	39.4689	25.1151	5.5661	91.346	1.2371	1.6743
					22	29.9013	39.4685	25.1149	5.5693	91.398	1.2098	1.8479
					23	29.9013	39.468	25.1146	5.5476	91.043	1.2169	1.8544
					24	29.9013	39.4674	25.1141	5.5504	91.088	1.1544	1.94
8	6-11-2015, 15:12:13.000	51.8995	25.90067	26	1	30.0277	39.3881	25.0108	5.8304	95.833	0.8243	1.0766
					2	30.0453	39.3878	25.0044	5.8419	96.049	0.8121	1.0855
					3	30.0498	39.3878	25.0029	5.8478	96.152	0.8244	1.0756
					4	30.0492	39.3881	25.0033	5.8581	96.321	0.817	1.0753
					5	30.0461	39.3879	25.0042	5.8658	96.444	0.8124	1.0839
					6	30.0433	39.3884	25.0055	5.8645	96.417	0.8046	1.076
					7	30.0453	39.3884	25.0048	5.8861	96.776	0.8074	1.081
					8	30.0455	39.3884	25.0048	5.876	96.61	0.7912	1.0695
					9	30.0135	39.3824	25.0113	5.8746	96.535	0.8209	1.0764

					10	29.947	39.3742	25.0282	5.8015	95.23	0.9057	1.0962
					11	29.9199	39.3727	25.0365	5.766	94.605	0.9741	1.1067
					12	29.9073	39.3713	25.0397	5.7746	94.726	0.9768	1.1011
					13	29.8935	39.3697	25.0433	5.7699	94.628	0.9761	1.1009
					14	29.8744	39.369	25.0494	5.7368	94.057	0.9783	1.0993
					15	29.8541	39.3687	25.0562	5.6391	92.424	0.9822	1.1756
					16	29.8501	39.3684	25.0574	5.6027	91.822	0.9767	1.1863
					17	29.8483	39.3682	25.0579	5.6066	91.883	0.9783	1.1929
					18	29.847	39.3681	25.0582	5.5964	91.714	0.9623	1.1923
					19	29.8457	39.3681	25.0587	5.5784	91.416	0.9136	1.1837
					20	29.8463	39.3683	25.0586	5.567	91.231	0.9263	1.1994
					21	29.8468	39.3684	25.0585	5.5471	90.906	0.9123	1.1996
					22	29.847	39.3682	25.0583	5.5531	91.004	0.9809	1.1985
					23	29.8473	39.3683	25.0583	5.5499	90.953	1.1006	1.2118
					24	29.8475	39.3683	25.0582	5.5419	90.821	0.9369	1.2335
8	6-11-2015, 20:53:00.000	51.89917	25.9005	26	25	29.848	39.3683	25.058	5.5003	90.14	0.9907	1.2066
					1	30.0972	39.4826	25.0577	5.7023	93.88	0.6583	1.0455
					2	30.1063	39.4827	25.0545	5.6853	93.613	0.6668	1.0449
					3	30.1059	39.4827	25.0547	5.6913	93.711	0.6509	1.0431
					4	30.1204	39.4845	25.051	5.6754	93.473	0.6255	1.0341
					5	30.1231	39.4843	25.0499	5.6908	93.73	0.617	1.0383
					6	30.1222	39.4836	25.0497	5.6841	93.617	0.6226	1.0346
					7	30.1201	39.4832	25.0502	5.6851	93.63	0.6412	1.0442
					8	30.122	39.4838	25.05	5.6821	93.585	0.6225	1.0412
					9	30.1204	39.483	25.0499	5.6726	93.426	0.6108	1.0363
					10	30.1206	39.4835	25.0502	5.6777	93.51	0.6088	1.0504
					11	30.125	39.4869	25.0512	5.6935	93.778	0.621	1.0391
					12	30.1246	39.4873	25.0517	5.6714	93.414	0.6174	1.047
					13	30.1236	39.4873	25.052	5.6814	93.577	0.6233	1.037
					14	30.1213	39.4884	25.0536	5.6788	93.531	0.6241	1.0356
					15	30.1198	39.4888	25.0545	5.6941	93.782	0.6163	1.0522
					16	30.1159	39.4894	25.0563	5.6894	93.699	0.6081	1.0427
					17	30.1111	39.4897	25.0582	5.6762	93.475	0.646	1.0562
					18	30.1043	39.4908	25.0614	5.6642	93.267	0.6122	1.0606
					19	30.0937	39.4899	25.0644	5.6472	92.972	0.6965	1.0926

					20	30.0285	39.491	25.0878	5.6201	92.43	0.7588	1.2247
					21	30.0182	39.4922	25.0923	5.4644	89.856	0.9202	1.4981
					22	30.0183	39.492	25.0921	5.5089	90.587	0.8925	1.5272
					23	30.0195	39.4916	25.0914	5.4929	90.325	0.914	2.0087
					24	30.0198	39.4914	25.0911	5.4956	90.37	0.9911	2.7017
					25	30.0201	39.4913	25.0909	5.4833	90.168	0.9782	2.8914
8	7-11-2015, 03:08:15.000	51.8995	25.90017	26	1	29.8614	39.3843	25.0655	5.3807	88.208	0.9756	1.6255
					2	29.8627	39.3845	25.0651	5.3638	87.931	0.8493	1.1024
					3	29.8618	39.3846	25.0655	5.3742	88.102	0.8698	1.1276
					4	29.8627	39.3847	25.0653	5.3709	88.048	0.8948	1.1051
					5	29.8673	39.3842	25.0633	5.3723	88.077	0.9066	1.1196
					6	29.8705	39.3842	25.0622	5.366	87.979	0.8973	1.143
					7	29.8708	39.3839	25.0619	5.3694	88.034	0.9048	1.1384
					8	29.8691	39.3841	25.0626	5.377	88.158	0.8365	1.1465
					9	29.8681	39.3841	25.063	5.3735	88.098	0.8591	1.14
					10	29.8652	39.3843	25.0641	5.3728	88.083	0.8695	1.1258
					11	29.874	39.384	25.0608	5.3591	87.871	0.92	1.1128
					12	29.8753	39.3836	25.0601	5.3779	88.18	0.8969	1.1344
					13	29.8758	39.3837	25.06	5.356	87.823	0.9281	1.1697
					14	29.8763	39.3836	25.0598	5.3781	88.185	0.9178	1.1483
					15	29.872	39.3839	25.0615	5.3664	87.987	0.9373	1.1395
					16	29.8698	39.3842	25.0625	5.3803	88.212	0.9299	1.164
					17	29.8714	39.3844	25.062	5.3842	88.279	0.9226	1.1377
					18	29.8726	39.3844	25.0616	5.3727	88.091	0.9018	1.1267
					19	29.8737	39.3845	25.0613	5.3721	88.084	0.9283	1.1425
					20	29.8731	39.3848	25.0618	5.3835	88.269	0.9498	1.1351
					21	29.8737	39.3848	25.0615	5.3839	88.276	0.935	1.1182
					22	29.8735	39.3847	25.0615	5.3721	88.084	0.9752	1.1473
					23	29.8735	39.3848	25.0616	5.3682	88.019	0.9011	1.2021
					24	29.8741	39.3848	25.0614	5.376	88.148	0.8777	1.2003
					25	29.8749	39.3847	25.0611	5.3706	88.06	0.9322	1.5054
7	7-11-2015, 07:36:44.000	51.89867	25.9515	20	1	29.8511	39.3773	25.0637	5.6415	92.465	0.8856	0.9897
					2	29.8392	39.3787	25.0689	5.615	92.012	1.1541	1.0266
					3	29.8546	39.3786	25.0635	5.6378	92.409	1.0403	0.9887

					4	29.8688	39.379	25.0589	5.6526	92.673	0.9879	1.0102
					5	29.8765	39.3791	25.0563	5.6717	92.997	0.938	0.9979
					6	29.8751	39.3795	25.0571	5.6724	93.006	0.946	0.9826
					7	29.8664	39.3791	25.0598	5.6769	93.067	0.9617	0.9796
					8	29.8393	39.3791	25.0691	5.6709	92.928	0.9819	1.0353
					9	29.8323	39.3791	25.0716	5.6356	92.34	1.1324	1.0124
					10	29.8133	39.3798	25.0787	5.6337	92.283	1.2509	1.0017
					11	29.8158	39.3789	25.0771	5.613	91.946	1.2191	0.9863
					12	29.8112	39.3792	25.0789	5.5934	91.619	1.2512	1.048
					13	29.8114	39.3792	25.0788	5.6002	91.73	1.2237	0.9891
					14	29.8123	39.3792	25.0785	5.6019	91.759	1.2097	1.0031
					15	29.8113	39.3789	25.0787	5.6016	91.752	1.1521	0.9881
					16	29.8109	39.3788	25.0788	5.5804	91.404	1.1548	0.9934
					17	29.8114	39.3789	25.0786	5.5947	91.64	1.1528	0.9994
					18	29.8121	39.3788	25.0783	5.5815	91.425	1.1142	1.0202
					19	29.8135	39.3788	25.0779	5.5781	91.371	1.1002	1.0092
10	7-11-2015, 09:18:36.000	51.76583	26.03433	27	1	29.9884	39.252	24.9221	5.8069	95.316	0.5839	1.05
					2	29.9407	39.2506	24.9375	5.8153	95.38	0.6	1.0491
					3	29.8899	39.2505	24.955	5.8041	95.12	0.6426	1.0706
					4	29.8836	39.2499	24.9568	5.7775	94.675	0.6856	1.0919
					5	29.8693	39.2488	24.9608	5.7912	94.877	0.7615	1.0816
					6	29.8382	39.2471	24.9702	5.7677	94.445	0.7719	1.0884
					7	29.8236	39.2451	24.9738	5.7454	94.057	0.7788	1.1325
					8	29.8114	39.2472	24.9796	5.7454	94.04	0.8636	1.1121
					9	29.8068	39.2479	24.9817	5.7381	93.914	0.9859	1.1175
					10	29.8061	39.2481	24.9821	5.721	93.632	1.0121	1.1568
					11	29.8045	39.2484	24.9829	5.722	93.647	1.0199	1.1583
					12	29.8035	39.2487	24.9834	5.7096	93.443	1.0367	1.1318
					13	29.7981	39.25	24.9863	5.7027	93.323	1.072	1.1473
					14	29.8021	39.257	24.9902	5.6566	92.578	1.289	1.1296
					15	29.8027	39.2604	24.9925	5.6184	91.956	1.3141	1.2571
					16	29.7989	39.2647	24.9971	5.5507	90.844	1.2454	1.2516
					17	29.7988	39.2648	24.9972	5.5173	90.297	1.2198	1.2549
					18	29.7982	39.2649	24.9975	5.5165	90.283	1.2412	1.3067
					19	29.7986	39.265	24.9974	5.5149	90.257	1.265	1.2691

					20	29.7984	39.2651	24.9976	5.5116	90.204	1.269	1.2836
					21	29.7982	39.2652	24.9977	5.4838	89.749	1.234	1.3295
					22	29.7985	39.2651	24.9975	5.4939	89.914	1.2671	1.2916
					23	29.7988	39.2651	24.9974	5.4803	89.691	1.2156	1.3369
					24	29.7989	39.2651	24.9974	5.4741	89.59	1.2968	1.3469
					25	29.7991	39.2651	24.9973	5.4746	89.599	1.1443	1.3707
					26	29.7996	39.2651	24.9971	5.4768	89.635	1.3382	1.303
9	7-11-2015, 11:14:34.000	51.69683	26.11833	18	1	30.0347	39.2338	24.8923	5.8134	95.484	0.7997	1.0638
					2	30.021	39.2334	24.8968	5.8078	95.371	0.8201	1.0774
					3	30.0097	39.2332	24.9006	5.8053	95.312	0.7905	1.0664
					4	30.0118	39.2336	24.9001	5.8133	95.447	0.7805	1.0681
					5	30.023	39.2334	24.8961	5.8173	95.529	0.7616	1.0659
					6	29.985	39.234	24.9097	5.8205	95.524	0.7534	1.0686
					7	29.947	39.2296	24.9195	5.8135	95.35	0.781	1.0783
					8	29.7143	39.2293	24.9996	5.764	94.19	0.9003	1.1103
					9	29.6847	39.231	25.0111	5.7351	93.674	1.0312	1.1329
					10	29.6821	39.231	25.012	5.7414	93.773	1.1198	1.1431
					11	29.6739	39.2338	25.0169	5.7143	93.32	1.1087	1.1546
					12	29.6673	39.2361	25.0209	5.6873	92.871	1.1759	1.1791
					13	29.6673	39.236	25.0208	5.688	92.883	1.1768	1.1647
					14	29.6672	39.236	25.0209	5.6883	92.886	1.2071	1.1593
					15	29.6671	39.2362	25.0211	5.6877	92.877	1.2203	1.176
					16	29.6664	39.2371	25.0219	5.6776	92.711	1.2094	1.1308
					17	29.6663	39.2377	25.0224	5.6695	92.579	1.2032	1.1854
					18	29.6672	39.2381	25.0224	5.6686	92.566	1.2109	1.1496